Spatial and temporal patterns of at-sea distribution and habitat use of New Zealand albatrosses

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Ode To An Albatross

The wind blows across the high seas
guiding the albatross
that is the course of the albatross:
crossing, descending, dancing, rising,
suspended in the darkness,
touching the towering wave,
nestling in the boiling mix
of unruly elements
as the salt decorates him
and the frenetic foam whistles,
the albatross slips by,
flying with his massive musical wings
leaving over the storm
a book that continues to fly:
it is the state of the wind

By Pablo Neruda
(Translation from Spanish: M. Tasker)

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ABSTRACT

Albatross populations are currently in decline around the world. Survival and reproduction of these large pelagic birds depends mostly on the conditions they encounter in their marine environment. Their ability to range far across ocean basins exposes them to a variety of anthropogenic threats. It is thus crucial to understand spatial and temporal patterns in the distribution and habitat use of each albatross species during different stages of their annual cycle in the context of seasonally changing demands as well as environmental constraints, in order to develop effective conservation measures. Using Global Location Sensing (GLS) loggers I investigated the non-breeding movements and habitat associations of three threatened or near-threatened albatross species breeding in New Zealand's Chatham Islands, the Chatham Albatross (*Thalassarche eremita*), Northern Buller's Albatross (*T. bulleri platei*) and Northern Royal Albatross (*Diomedea epomophora sanfordi*), within South American waters. Chatham and Northern Buller's Albatrosses mainly occupied waters with mean sea surface temperatures (SST) of 17-18ºC along the coasts of Chile and Peru, while Northern Royal Albatrosses were mostly found in 10-12ºC waters off southern Chile and Argentina. Monthly movement patterns were linked to seasonal shifts in temperature range, suggesting SST was an important environmental factor in explaining the observed spatial and temporal patterns. GLS loggers were also applied to study the patterns of movement and habitat use of Chatham Albatrosses when migrating across the South Pacific between breeding and non-breeding grounds. The route and timing of migration were consistent over the three year period of the study, although subject to individual variation. Stopovers on migration were found to be common, lasting between 3 and 26 days. Activity patterns suggested that birds stopped in order to forage *en route*. Lastly, I used high resolution Global Positioning Sensing (GPS) loggers to address the fine-scale movements and habitat selection of foraging Chatham Albatrosses over three years during early chick rearing. This is a time when their behaviour is expected to respond to increased energetic demands as they are feeding young chicks. Foraging trips lasted between 1 and 6 days and the foraging range rarely exceeded 400 km. The location of potential foraging spots varied between years, but followed non-random patterns in bathymetry, slope, SST and Chlorophyll a. The results presented here suggest that albatrosses rely on predictable habitat features but are flexible to respond to fine scale changes within their marine environment. The dynamic nature of both birds and environment may prove challenging but has to be taken into account in conservation planning.

CHAPTER 1

Introduction

As most seabird species rely entirely on the marine environment for providing the food resources necessary for reproduction and survival, it is crucial to understand how they use this environment both temporally and spatially in order to assess and mitigate any potential anthropogenic threats which may be encountered out at sea. Amongst the Procellariiformes (albatrosses, shearwaters and petrels), a diversity of movement and dispersal strategies exists, ranging from being resident all year round, through to transequatorial and circumpolar migrants (e.g. Mackley et al. 2010) . What is unusual amongst this group is their ability to cover large distances in very little time and how they integrate inshore, shelf and spatially distinct offshore areas into their general habitat through their annual movements (e.g. Weimerskirch and Wilson 2000; Shaffer et al. 2006). This provides them with access to a variety of habitats and may allow compensation for temporal variation in food abundance. What drives the actual choice of habitats in seabirds out at sea is subject to much study and in recent years this research has become important in identifying potential threats according to what areas species exploit during the different stages of their annual cycle (Burger and Shaffer 2008).

In the last two decades, a better understanding of the movements of seabirds and their habitat requirements, have taken on new urgency. The spatial ecology of animals has been identified as one of six high priority research areas in seabird conservation science (Lewison et al. 2012). Amongst just the albatrosses, for example, 19 out of 22 species are currently considered threatened or near-threatened (BirdLife International 2004). In some cases, the decline is associated with habitat loss, pollution and the introduction of invasive animals onto their nesting islands (Taylor 2000). However, for most albatross species, the primary cause of their endangerment appears to be increased adult mortality associated with commercial fisheries (Croxall et al. 2012). Understanding the movements of albatrosses and how these vary over time (both in terms of their breeding cycles but also the level of consistency over a number of years) is critical to planning mitigation measures by the fishery industry, whether this is simply avoiding high use areas of albatrosses or ensuring best fishery practises are implemented in areas which are of importance for albatrosses. Due to naturally low population numbers and low reproduction rates, adult mortality has a particularly strong impact on population dynamics. Many species are in decline (Croxall et al. 2012) and the delayed sexual maturity and high adult longevity, and thus slow reproduction that is characteristic of this taxon, leads to adult mortality having a particularly strong impact on population numbers.

New Zealand is an archipelago of over 330 islands and has one of the largest Exclusive Economic Zones (EEZs) of any country. This vast EEZ is of crucial importance for albatrosses, with this area having breeding populations of 13 of the 22 taxa, of which 9 are endemic breeders (Taylor 2000). As knowledge on their population status as well as habitat use and potential overlap with commercial fisheries within New Zealand waters is still deficient, and in the light of globally declining albatross populations, monitoring and recovery plans have been implemented in many species (e.g. NPOA-Seabirds; Taylor 2000) in order for future conservation planning. The three albatross species studied in this thesis, Chatham Albatross (*Thalassarche eremita*), Northern Buller's Albatross (*T. bulleri platei*) and Northern Royal Albatross (*Diomedea epomophora sanfordi*) are endemic to New Zealand and subject to national and international seabird conservation planning and research. My objective was to answer questions about the distributional patterns of these species of albatrosses at sea on both spatial and temporal scales. One particular aim was to provide a year-round overview of which areas become of importance at different stages of the annual cycle and discern what influences, but also explains, the distributional as well as the behavioural patterns observed. Such information would allow a better understanding of when and where conservation action may be needed. It is hoped that the new insights into distributional patterns this work will provide, will be of benefit to the conservation of albatrosses and in particular to New Zealand's role in this respect.

Chatham, Northern Buller's and Northern Royal Albatrosses all breed sympatrically in the Chatham Island group, about 800 km to the east of New Zealand's South Island. Their breeding sites are thus located within the far stretching continental shelf, the Chatham Rise, which is known for its highly productive marine environment and accordingly is one of New Zealand's most intensely used fishing grounds. Knowledge on the location of each species while out at sea has been fairly sparse to date, derived from ship-based observations and preliminary satellite tracking studies conducted on Chatham Albatrosses and Northern Royal Albatrosses in the 1990s (Robertson et al. 2000; Nicholls et al. 2002; Spear et al. 2003; BirdLife International 2004; Latham et al. 2004; Nicholls et al. 2005; Nicholls 2007; Nicholls and Robertson 2007). This work indicated that the species leave their breeding environment during the non-breeding season to migrate across the South Pacific and become resident in South American waters. The location varied across species, with the Chatham Albatrosses remaining in Chilean and Peruvian waters during non-breeding, while Northern Royal Albatrosses were found in both Chilean and Argentinean waters. As the satellite tracking

devices had a limited battery capacity and were thus prone to fail prematurely, only a few records of return trips to the breeding colonies exist, suggesting that Chatham Albatrosses return via the South Pacific, while at least some Northern Royal Albatrosses had circumnavigated the globe on return at their breeding grounds. These results, however, were based on small sample sizes and provided little information on whether these were consistent patterns for the species, or how the non-breeding habitat was utilized. No information on the distribution of Northern Buller's Albatrosses had been published prior to the present work, mainly due to the difficulty in distinguishing between the Northern and the closely related Southern Buller's Albatross (*T. bulleri bulleri*). Although 'Buller's Albatrosses' have been observed within Chilean and Peruvian waters (Spear et al. 2003), no tracking studies have been carried out on the *T. bulleri platei* population of the Chatham Islands (here referred to as Northern Buller's Albatross). Nevertheless, based on this fragmentary information, it appears that all three study species spend the sedentary part of their non-breeding period in highly productive water regimes (i.e., Humboldt Current System along South America's west coast and the Patagonian Shelf in Argentina), which like their breeding region are intensely used by fishing operations. Thus, the species are facing high potential risks from fisheries during at least two stages of their annual cycle.

Given the potential threats to all three species over such a wide geographical area, it is critical to define areas of importance to the birds in more detail and identify whether these areas remain consistent or are subject to change over time. Paramount to defining areas of importance is determining what features characterise these areas and why or how they are used by different species. Thus, I also investigated physical processes in relation to the spatial and temporal patterns of the study species, in order to evaluate how this information can be used for albatross conservation. I divided my research into three distinct stages within the annual cycle of the study species, namely 'breeding', 'migration' and 'non-breeding,' to find out how distributional patterns and behaviour change over the course of the year. During breeding the birds are spatially constrained and under high energy demands when raising chicks (Pinaud and Weimerskirch 2005; Young 2009). How does this affect the timing and location of their foraging trips? On migration birds commute long distances between breeding and non-breeding areas, traversing the high seas of the South Pacific. Is this done by the most direct route to minimize time, or do individuals forage along the way as has been found in other species (Egevang et al. 2010; Klaassen et al. 2012) in order to reduce energy expenses? Do birds make use of their marine environment on migration? Finally, when birds arrive in

the non-breeding areas, habitat can be selected over a larger geographical area compared to the spatial constraints associated with breeding. What influences habitat selection during non-breeding? Do species from common breeding sites segregate during that period?

Recent advances in technology mean that some of the questions posed above can now be addressed using data logging systems that allow one to track birds over long distances and long periods of time. The use of two different positional data logging systems enabled me to address questions on different spatial as well as temporal scales. Global Location Sensing (GLS) devices were used to cover the migration and non-breeding periods due to their extended battery life. Although they are limited in the precision of positional data, their integrated salt water immersion and temperature sensors provided valuable information on bird activity and environmental *in situ* measurements, which otherwise would have been hard to gather. Global Positioning System (GPS) loggers, which record positions at a much higher resolution, were used to identify fine scale movements during breeding, when the birds were ranging in spatially limited areas. This work only focussed on adult breeding birds due to the logistic issues in reliably retrieving data loggers from the study birds. While on eggs or small chicks, the albatrosses appeared to have a very strong bonding to their nest and could be easily approached.

In the following sections I give an overview on the general breeding biology and protection status of each of the three study species as background information. I then follow with an outline of research goals addressed in the subsequent chapters of the thesis.

SPECIES DESCRIPTION

Chatham Albatross (*Thalassarche eremita*)

The Chatham Albatross is endemic to New Zealand, breeding only on The Pyramid in the southern outskirts of the Chatham Islands (Figure 1). The location as well as the forbidding character of the breeding island limit the time during which research can be carried out, resulting in substantial gaps in the basic knowledge of the biology of this species.

Population estimates and breeding biology

Breeding on a single island of limited size (1.7 hectares) and precipitous terrain, population numbers of the Chatham Albatross have to be considered as being naturally low. Population estimates based on aerial photography and spot-check ground counts in the 1970s and 1990s in combination with repeated whole island ground counts during recent years (Robertson et

al. 2003a; Scofield 2006; Scofield et al. 2007b; Fraser et al. 2008b; Fraser et al. 2009b) found annual breeding numbers to remain considerably stable, ranging around 4,600 breeding pairs. Whole population counts including non-breeding and immature birds did not prove feasible on the ground, but aerial photography from the 1970s resulted in estimates of a total population of about 18,000-20,000 individuals (Gales 1998). Adult breeding birds have been banded since 1974 and the oldest Chatham Albatross accounted for was at least 34 years of age when last seen in 2001 (Robertson et al. 2003a). The mean survival rate of adult breeding birds has been calculated to be 86.8% (Robertson et al. 2003a). As pointed out in the current ACAP report on the species (ACAP 2009b), this level of survival is comparatively low for albatrosses and may suggest a declining rather than a stable population, although there have been no major changes in nesting number over recent years. Since albatrosses are long-lived and reproduction is slow, long-term monitoring is needed to detect changes in population numbers and reproductive success.

Chatham Albatrosses breed annually, raising a single chick, with both parents participating in incubating, chick rearing and guarding. Eggs are laid September-October, hatching occurs in November-December and young fledge in March-April (ACAP 2009b). Incubation stints take 2-3 days on average but can vary between 0.5 and 8 days (Robertson et al. 2003a; BirdLife International 2004). Birds start returning to the colony at the age of four but do not commence breeding before the age of seven (Robertson et al. 2003a). On average, 60% of available nest sites are occupied during incubation and early chick rearing (October – December; Robertson et al. 2003a; Scofield et al. 2007b; Fraser et al. 2008b; Fraser et al. 2009b). No reliable data are available on initial numbers of eggs laid and final breeding success. Estimates are that between 1,200 and 2,900 chicks successfully fledge each year (Croxall and Gales 1998).

Conservation status

The Chatham Albatross is listed as ‘vulnerable’ by the IUCN (www.iucnredlist.org, version 2011.1.) The species was only recently downlisted from ‘critically endangered’ (in 2010) since the assumed threat of ongoing habitat degradation at its single breeding site did not becoming evident after several years of ongoing monitoring, as well as population estimates remaining stable. It is still considered ‘vulnerable’ because the small size of the breeding site renders it susceptible to stochastic events and human impacts. In recent New Zealand threat rankings the Chatham Albatross has been listed as ‘naturally uncommon’ (Miskelly et al. 2008). The species is subject to monitoring and research under the New Zealand NPOA-

Seabirds (Taylor 2000) and the recovery plan for albatrosses in the Chatham Islands (Department of Conservation 2001, 2004).

Northern Buller's Albatross (*Thallassarche bulleri platei*)

The Northern Buller's Albatross is endemic to New Zealand, breeding in the Chatham Islands (The Forty-Fours and The Sisters; Figure 1) and Three Kings Islands (Rosemary Rock). The status of this taxon as a full species remains disputed (Robertson and Nunn 1998; Brooke 2004; Onley and Scofield 2007), and neither IUCN (www.iucnredlist.org, version 2011.1.) nor ACAP (2009a) distinguish between Northern (*T. bulleri platei*) and Southern (*T. bulleri bulleri*) subspecies. However, following Miskelly et al. (2008) and Taylor (2000), the Northern Buller's Albatross will be treated as distinct from the Southern Buller's Albatross for the purpose of this study. This is mainly due to the two taxa inhabiting geographically fairly distinct breeding sites, resulting in differing breeding schedules (ACAP 2009a), and potentially different behaviour and distribution at sea.

Population estimates and breeding biology

About 90% of the Northern Buller's Albatross breeding population is located on The Forty-Fours in the Chatham Islands. Population estimates based on observations during recent decades indicated a breeding population of about 18,000 pairs (Gales 1998), of which 14,000-16,000 are assumed to breed on the Forty-Fours (Robertson 1991; Scofield 2005; ACAP 2009a). Since The Forty-Fours, as The Pyramid, present challenging conditions regarding extended field research, data on the breeding biology of the Northern Buller's Albatross are limited. Very little data exist on the survival rates of the species. Based on observations on Little Sister, mean adult survival between 1974 and 1995 was calculated to be 93% (Robertson et al. 2003b; ACAP 2009a). There are no survival estimates for birds breeding on the Forty-Fours. The age of first return to the colony is not known.

Northern Buller's Albatrosses are annual breeders and commence egg laying in October/November, with chicks hatching in January and fledging in June/July (ACAP 2009a). Both partners are involved in incubation and chick rearing. Incubation lasts about 70 days (Department of Conservation 2001), and mean incubation shifts are 2-4 days long with a maximum of 9 days (Robertson and Sawyer 1994). Nest occupation of about 90% during egg laying was observed to be the norm during ground counts on The Forty-Fours in 2007, 2008 and 2009 (Scofield et al. 2007a; Fraser et al. 2008a; Fraser et al. 2009a). Recorded failure rates from those visits ranged between 3 and 9%. According to Robertson and Sawyer (1994)

egg failure was sometimes due to poor nests built on sharp rocks, which was an exacerbated issue after severe storms removed most of the topsoil from the Sister and Forty-Fours in the mid 1980s. No reliable data exist on breeding success.

Conservation status

The (Northern) Buller's Albatross is listed as 'near threatened' by the IUCN (www.iucnredlist.org, version 2011.1.), although no distinction is made between Northern and Southern subspecies. The status is based on the population being stable and the breeding islands being sufficiently widespread, which is considered to limit the likelihood of becoming highly threatened owing to human activities or stochastic events. According to New Zealand's recent threat rankings, the Northern Buller's Albatross is seen as 'naturally uncommon' (Miskelly et al. 2008). The species is subject to monitoring and research under the New Zealand NPOA-Seabirds (Taylor 2000) and the recovery plan for albatrosses in the Chatham Islands (Department of Conservation 2001, 2004).

Northern Royal Albatross (*Diomedea epomophora sanfordi*)

The Northern Royal Albatross is endemic to New Zealand, breeding in the Chatham Islands (The Forty-Fours and The Sisters; Figure 1) and on Taiaroa Head near Dunedin.

Population estimates and breeding biology

The majority of Northern Royal Albatrosses is found in the Chatham Islands with an estimated 5,200-5,800 annual breeding pairs, while Taiaroa Head holds about 30 pairs, though this same mainland population includes some hybrids with Southern Royal Albatrosses (Gales 1998; ACAP 2009c; BirdLife International 2009). Due to the biennial breeding cycle of Northern Albatrosses, where birds which have successfully raised a chick usually do not return to their breeding colony for another year, whilst those who failed will attempt to breed again in the following season (Robertson 1998; ACAP 2009c), variability in annual breeding numbers is generally high and counts over a series of consecutive years are necessary to establish population trends. Moreover, since The Forty-Fours and The Sisters present challenging conditions regarding extended field research, data on the breeding biology of the Northern Royal Albatross from those sites are limited. While breeding numbers at Taiaroa head are still increasing (not least due to intense monitoring and management), the population of the Chatham Islands was thought to undergo a decline after severe storms in the 1980`s destroyed albatross nesting habitat and removed big proportions

of soil and plant material needed to rebuild nests. The mean annual productivity dropped from 54% recorded in the 1970s to 18% during the 1990s (Robertson and Sawyer 1994; Robertson 1998; BirdLife International 2009). More recent visits to the Chatham Islands found that the vegetation and soil on both The Forty-Fours and The Sisters was recovering and that the annual number of breeding pairs on eggs was at the same level as before the storms (Scofield 2005; BirdLife International 2009).

Northern Royal Albatrosses lay their eggs between October and December, and these hatch in January/February and fledge in September/October (ACAP 2009c). Incubation takes on average 79 days and rearing the chick requires an additional 240-250 days. All duties are shared by both parents and incubating and guarding stints are 2-4 days on average (Gales 1998; BirdLife International 2004; ACAP 2009c). Immature birds start returning to the colony at an age of 3-4 years but do not commence breeding before 6-8 years of age (Robertson 1998; ACAP 2009c). The mean annual adult survival of Northern Royal Albatross does not differ much between breeding sites at Taiaroa Head and on the Chatham Islands, with 94.6% and 95.2%, respectively (Robertson 1998; ACAP 2009c). Juvenile survival at Taiaroa Head is estimated to be 69% (ACAP 2009c). No such data are available for the Chatham Island birds.

Conservation status

The Northern Royal Albatross is listed as 'endangered' by the IUCN (www.iucnredlist.org, version 2011.1.), based on its restricted breeding range and the recent event of habitat degradation due to severe storms in the 1980's, followed by declines in annual productivity. New Zealand lists the species as 'naturally uncommon' (Miskelly et al. 2008). Northern Royal Albatrosses are subject to monitoring and research under the New Zealand NPOA-Seabirds (Taylor 2000) and the recovery plan for albatrosses in the Chatham Islands (Department of Conservation 2001, 2004).

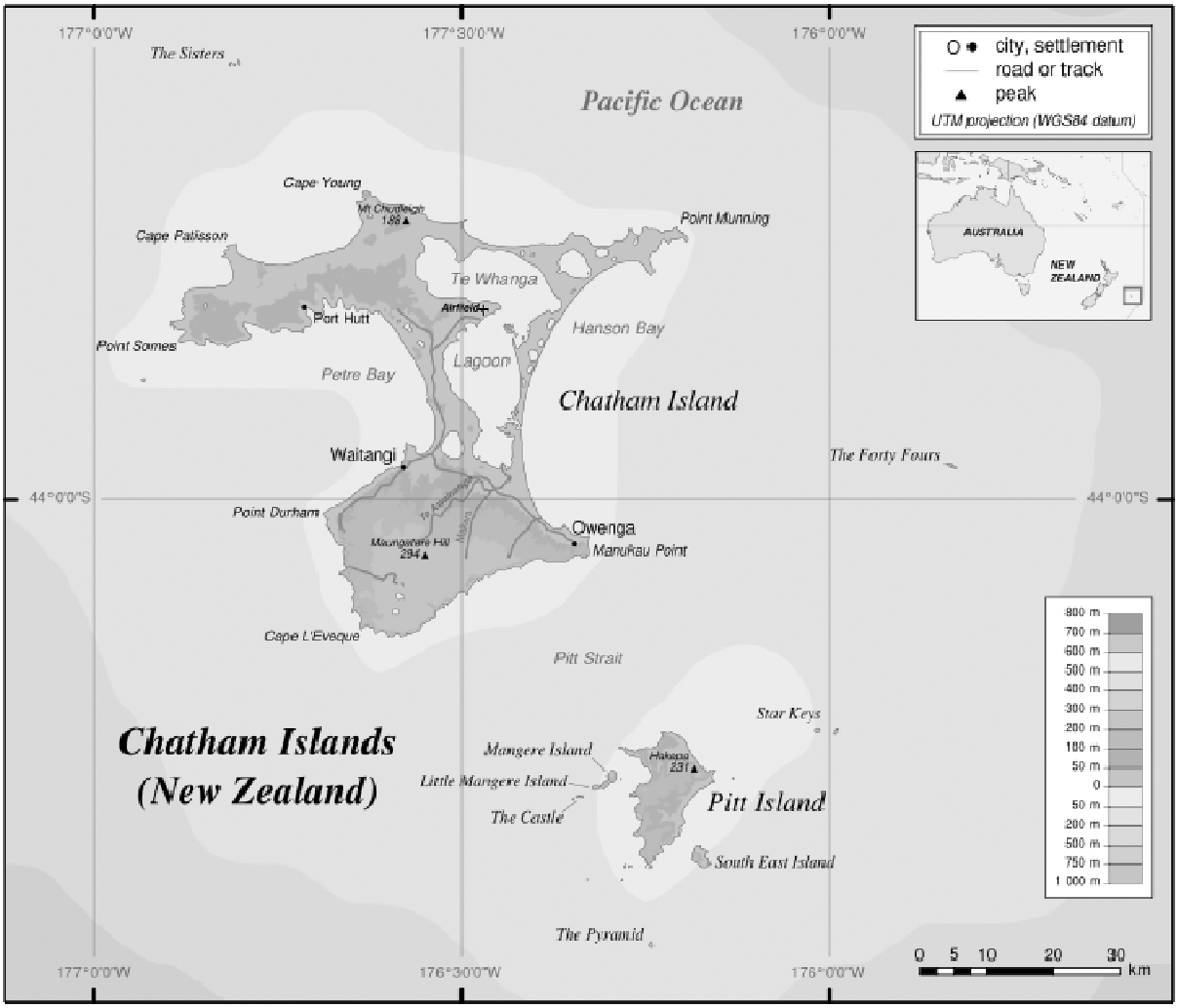

Figure 1: Map of the Chatham Islands (adapted from http://en.wikipedia.org/wiki/Chatham_Islands).

THESIS OUTLINE

The following chapters address the spatial and temporal dynamics of movements within each of the three stages of the annual cycle of the three albatross species studied. My goal was to firstly, describe the movements of birds while at sea, and secondly to understand the environmental factors that might be driving the selection of particular areas used by the birds in each of the different stages of their annual cycle. By highlighting the dynamic nature of the movements in these species, I hoped to contribute to a better understanding on how albatrosses utilize their marine environment under seasonal changing constraints. The fact that two out of three chapters deal with patterns observed during the non-breeding season, reflects my desire to emphasize those parts of the annual cycle for which knowledge is still comparatively sparse. Although my research questions are mainly addressed on the species level (more suitable with regard to the underlying strong conservation perspective), individual variation is taken into account in the interpretation of the data where appropriate. The results of this thesis not only complement and add to the preliminary and patchy information already available for the species studied, but also provide a baseline for future research of these threatened species. It is hoped that the results will inform conservation planning and aid in the designation of protected areas as well as implementation of mitigation measures in the marine environment.

In **Chapter 2**, based on GLS (geolocation) tracking data and the temperature recordings provided by the built-in salt water immersion sensors of these loggers, I investigate how Chatham, Northern Buller's and Northern Royal Albatrosses spatially segregate when at their non-breeding grounds along the coasts of South America. I also show that movements of the birds observed within these areas are linked to sea surface temperature (SST) over space and time, and demonstrate whether and how this differs between species. This approach allows the identification of local oceanic temperature regimes in relation to bird distribution at a much higher precision than would have been possible by overlaying GLS tracking data and remotely sensed SST data, which are both comparatively coarse in spatial resolution. The study is the first to provide substantial reliable data on the non-breeding distribution of Northern Buller's Albatross and Northern Royal Albatross from the Chatham Island population.

In the next two chapters, I focused exclusively on the movements of the Chatham Albatross. This species seemed to be the ideal model for studying both localised movements

around the breeding colony (since the species is restricted to just one island) and on migration between the breeding and non-breeding grounds. In **Chapter 3,** I describe the spatial patterns on migration to and from the species' non-breeding grounds off the coast of South America, and the strategies used by the birds as they exploit the marine environment on migration. Using GLS tracking data from three consecutive years, I analyse the course, timing and duration of post-breeding and pre-breeding migrations as well as stopover behaviour while birds commute between their breeding and non-breeding grounds. Utilizing the built-in immersion sensors of the GLS loggers to derive information on the activity states of Chatham Albatrosses on migration, I investigate differences in behaviour between stopovers (periods in which the birds are temporarily sedentary) and sections of continuous migration to identify whether stopovers are used for foraging while birds are in transit.

The spatial and temporal patterns in habitat use of foraging Chatham Albatrosses and how this is related to a number of potentially key environmental characteristics during three consecutive breeding seasons are addressed in **Chapter 4**. Here I answer questions about habitat choice by adult birds during the early chick rearing phase by linking bird locations retrieved from tracking studies using high resolution GPS loggers to different habitat parameters (bathymetry, slope, SST and Chlorophyll a concentration) within potential foraging areas. I investigate the annual variability in these environmental associations as well as in the extent of the general foraging range and trip durations to evaluate consistency in the distributional patterns over time.

Finally, in **Chapter 5**, I provide a synthesis of my major findings. I conclude by discussing the findings within the wider context of albatross conservation biology, particularly in terms of applications within the marine environment. The conservation implications of my work are addressed and I end by giving suggestions for future research.

Note that chapters 2 - 4 have been written in manuscript style in anticipation of submitting them for publication, and are thus designed to be read independently. As a consequence, a certain amount of repetition was inevitable in order to give sufficient background to each chapter.

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CHAPTER 2

The relationship between sea surface temperature and the non-breeding distribution of three species of New Zealand albatrosses off the coast of South America

ABSTRACT

Sea surface temperature (SST) has been proposed to be a key environmental factor in explaining the distribution and habitat use of seabirds through its link to prey occurrence and availability, which in turn may ultimately dictate how species spatially segregate. Using Global Location Sensing (GLS) loggers with built-in temperature sensors and remotely sensed SST data, I studied the spatio-temporal movement patterns of three albatross species (Chatham Albatross, *Thalassarche eremita*, Northern Buller's Albatross, *T. bulleri platei*, and Northern Royal Albatross, *Diomedea epomophora sanfordi*) from the Chatham Islands, New Zealand at their non-breeding grounds along the coasts of South America. All three species remained within areas delimited by their predominantly used SST ranges. Chatham and Northern Buller's Albatrosses mainly occupied waters of 17-18ºC within a latitudinal range of 9ºS to 43ºS and 9ºS to 33ºS, respectively, off Chile and Peru. In comparison, Northern Royal Albatrosses frequented significantly cooler waters, mostly occuring at temperatures of 10-12ºC within more southerly areas off both the Chilean and Argentinean coasts (36ºS to 54ºS). The monthly movements of Chatham and Northern Buller's Albatrosses tracked the course of their preferred temperature ranges when cooler waters were transported northwards along the South American coasts during the course of the non-breeding periods. This study highlights how GLS in combination with *in situ* SST measurements can provide greater detail on how species utilize their marine habitat during non-breeding as well as identifying important marine areas for albatrosses at sea.

Key Words: Sea surface temperature, non-breeding areas, spatial and temporal distribution, habitat selection, albatross, GLS.

INTRODUCTION

The distribution of marine birds while at sea is influenced by a variety of physical and biological parameters. The abundance and availability of prey is considered to be one of the main drivers of habitat selection in seabirds and this in turn is likely controlled by a variety of environmental variables (Vilchis et al. 2006). In addition, the distribution of marine prey resources over space and time is often patchy and to forage successfully in such a vast and heterogeneous habitat, seabirds appear to follow a number of environmental cues to facilitate their search for prey (Waugh and Weimerskirch 2003; Bost et al. 2009). Research on habitat selection in seabirds has shown that oceanographic parameters such as bathymetry, sea surface temperature (SST), sea surface height anomalies, primary productivity and salinity correlate with distribution and behaviour (Hyrenbach et al. 2007; Bost et al. 2009; Rayner et al. 2011) and have been used to explain spatial and temporal patterns (Adams et al. 2010). In comparative studies, SST often emerges as the most relevant explanatory variable of seabird distribution (Reese and Brodeur 2006; Sandvik et al. 2008; Bost et al. 2009; Kappes et al. 2010; Nur et al. 2011), because it shows a relationship with primary producer biomass (O'Hara et al. 2006) and may indirectly affect seabirds through trophic cascades (Luczak et al. 2011). Sea surface temperature may further function as a cue for locating prey (Trathan et al. 2008). However, temperature is also known to influence the distribution of fish via processes that do not involve changes in primary productivity (Devney et al. 2009), and thus the importance of temperature independent from other potential environmental drivers should also be taken into account when trying to understand the distribution and movements of seabirds.

Recently, concern over the consequences of climate change (e.g. global warming; more frequent El Niño events) has made the monitoring and understanding of processes linking seabirds and ocean temperature even more crucial. Large changes in sea temperatures can have major impacts on marine food webs (Slater and Byrd 2009) and affect seabirds through changes in adult survival, time of breeding, or breeding success (Chambers et al. 2011). In the southern hemisphere, warming seas were found to cause poleward shifts in the distribution of Wandering Albatrosses (*Diomedea exulans*) and a number of species of Prions (*Pachyptila* spp.; Péron et al. 2010, Quillfeldt et al. 2010), indicating the ability of at least some seabird species to respond quickly to changing conditions in ocean climate.

Despite the evidence for responsiveness in some species to changing ocean climate, the results of studies on how environmental variables influence the behaviour and distribution of

seabirds have been inconsistent (Hamer 2010). Other factors have been suggested to affect these patterns, such as whether species are targeting fish/squid or are planktivorous, as well as whether or not birds are restricted to foraging within the range of their breeding colonies or if they venture more widely during the non-breeding season (Vilchis et al. 2006). Habitat conditions, including species-specific habitat requirements, are subject to change through the different stages in the annual cycle of a species as well as in different parts of its geographical range (e.g. breeding and non-breeding grounds; Rolland et al. 2008). Even within the same geographic range, the distributions of different species can vary according to different patterns in specific associations with environmental parameters (Bugoni et al. 2008).

Environmental conditions in non-breeding areas are known to have an important influence on survival and the onset of reproduction in the following season (Nevoux et al. 2007; Schroeder et al. 2009; Rivalan et al. 2010), and ocean temperatures, in particular, appear to be one of the principal factors influencing these key life-history traits (Sandvik et al. 2005; Raya Rey et al. 2007; Rayner et al. 2011). For far ranging species like albatrosses and petrels, which can cross entire ocean basins on migration (Burger and Shaffer 2008), it is important to identify the movements of birds in concordance with their habitat requirements in both the breeding and non-breeding seasons. The pelagic lifestyle and surface-feeding behaviour of many species of albatross suggests that SST is likely to be a key factor in delimiting distributions in this group. For example, Louzao et al. (2010) found the placement of key pelagic habitats for albatrosses in the southern Indian Ocean to be dependent on SST and Kappes et al. (2010) likewise identified SST as the most important variable for predicting the search effort of albatrosses in sub-tropical waters.

In this study I focus on the movements of three species of albatrosses within their non-breeding ranges in the South Pacific: Chatham Albatross (*Thalassarche eremita*), Northern Buller's Albatross (*T. bulleri platei*), and Northern Royal Albatross (*Diomedea epomophora sanfordi*). These species are endemic to New Zealand and breed sympatrically in the Chatham Islands. Until recently, Chatham Albatrosses were thought to venture no further than the central Pacific (Reid and James 1997), with rare records from Australia, South Africa and South America (Haase 1994; Reid and James 1997; Ryan 2002). However, ship-based investigations and satellite-tracking studies in the 1990's identified the Pacific coast of Chile and Peru as the main area frequented by this species during the non-breeding season (Robertson et al. 2000; Spear et al. 2003; BirdLife International 2004; Latham et al. 2004; Nicholls and Robertson 2007). Northern Royal Albatrosses, likewise studied via satellite-

tracking in the 1990's, also travel to South American waters during their non-breeding period (Nicholls et al. 2002), with most birds residing on the Patagonian Shelf of Argentina, and some birds staying along the coast of southern Chile (Nicholls et al. 2002; BirdLife International 2004; Nicholls et al. 2005; Nicholls 2007). According to ship-borne observations, Buller's Albatrosses also frequent waters off Chile and Peru during the austral winter (Stahl et al. 1998; Stahl and Sagar 2000; Spear et al. 2003; ACAP 2009a), but such studies did not distinguish between the Northern and Southern subspecies of Buller's Albatross. Preliminary results from tracking studies of Southern Buller's Albatrosses (*T. b. bulleri*) recently confirmed the occupation of South American waters by this subspecies during non-breeding (Sagar et al. 2010), while no individual tracking data exist to date for the Northern Buller's Albatross.

Analysis of distributional data has identified the Humboldt Current System and the Patagonian Shelf as areas of intensive use by a number of albatross species (BirdLife International 2004), within which species were distributed heterogeneously according to environmental factors (Spear et al. 2003). Based on ship-borne observations, Spear et al. (2003) identified SST as the most important factor that determined the distribution of both Chatham Albatrosses and Buller's Albatrosses during the austral spring and autumn. However, no information exists on how the distributions of these species relate to SST on a temporal scale. Nicholls et al. (2002) related the distribution of Northern Royal Albatrosses in their non-breeding areas to bathymetric features but it is unclear whether the distribution of this species is also influenced by SST patterns as hypothesized for Chatham and Buller's Albatross.

The aim of this study was to determine how the distribution of the three species of albatross is linked to SST over space and time, and how this differs between species, by using archival tracking devices (Global Location Sensing; GLS) with water temperature sensors that provide accurate *in situ* temperature measurements via the bird. Specifically, I tested whether SST was linked with the distribution of albatrosses within their non-breeding ranges on a monthly scale, to investigate the importance of this habitat variable in explaining the movements and distribution of each species. In this study I focus on SST only, since correlating low resolution positional data (as retrieved from the GLS loggers) with parameters like bathymetry or primary productivity (Chl *a*), which change along comparatively fine scales off the South American west coast, was unlikely to give meaningful results. For SST however, I had access to temperature data recorded at the exact location of

the birds (via the sensors of the logger) and thus reliable information on the temperature ranges in which the study species actually occurred.

METHODS

Study sites and study species

Albatrosses were studied at their breeding sites on The Pyramid (44°25'S, 176°14'W) and The Forty-Fours (43°57'S, 175°50'W), Chatham Islands, New Zealand. Within the Chathams, The Forty-Fours hold the majority of Northern Royal Albatross and Northern Buller's Albatross populations, whilst The Pyramid is the world's only breeding site for the Chatham Albatross. Chatham Albatrosses and Northern Buller's Albatrosses are annual breeders whereas Northern Royal Albatrosses breed biennially, although they may attempt breeding in consecutive years if unsuccessful (Robertson 1998). All three species have comparatively small populations, with estimates of annual breeding pairs of 4,600 Chatham Albatrosses, 16,800 Northern Buller's Albatrosses, and 5,800 Northern Royal Albatrosses (ACAP 2009b, a, c). They are listed as 'vulnerable', 'near threatened' and 'endangered', respectively, by the IUCN (www.iucnredlist.org, version 2011.1.) and as 'naturally uncommon' in recent New Zealand threat rankings (Miskelly et al. 2008). They are subject to monitoring and research under the New Zealand NPOA-Seabirds (Taylor 2000) and the recovery plan for albatrosses in the Chatham Islands (Department of Conservation 2001, 2004).

Logger deployment and processing

Albatrosses were studied at their breeding sites on The Pyramid (44°25'S, 176°14'W) and The Forty-Fours (43°57'S, 175°50'W), Chatham Islands, New Zealand. In November/December 2007, 21 Chatham Albatrosses, 19 Northern Buller's Albatrosses and 10 Northern Royal Albatrosses were fitted with Global Location Sensing (GLS) loggers. The devices (GLS-Mk5, 18 x 18 x 6.5 mm, 3.5 g, battery life ~ 6 years) were built by the British Antarctic Survey (BAS). They were set to record date, time, light intensity, immersion in seawater, and water temperature. Light levels were measured every 60 s, and the maximum value over each 10 min recording interval was logged. Temperature was recorded after a 20 min period of continuous immersion, as it takes 10 min for the temperature sensor reading to stabilize (temperature sensor accuracy ± 0.5°C, with a resolution of 0.125°C (Fox 2009). Temperature was recorded again after 40 min, and repeated every 4 hours in cases of continuous

immersion (Fox 2009). The GLS loggers were attached to plastic leg rings, using liquid nail glue and steel-reinforced cable ties, and then placed on the tarsi of the selected birds while they were either incubating or chick rearing. The total weight of the attachment was 7 g, corresponding to about 0.1 - 0.2% of the average body mass of each species, and hence below the recommended threshold of 3 %, above which adverse behavioural effects can be expected (Phillips et al. 2003). All birds were also fitted with a numbered metal ring and their nest sites were tagged for identification, to allow recapture of returning birds over subsequent years. To ensure optimal retrieval rates, only adult breeding birds were chosen for this study, as they were more likely to be recovered at the same nest location than non-breeding adults or immature/prospecting birds. Logger retrieval rates were 70 % (15 loggers) for Chatham Albatrosses, 79 % (15 loggers) for Northern Buller's Albatrosses and 80 % (8 loggers) for Northern Royal Albatrosses. Non-retrieved loggers were either lost (e.g. dropped off bird) or individuals were not recovered (e.g. did not return to study site while field teams were present).

All retrieved GLS loggers provided tracking data over the course of the whole deployment period. Each dataset was analysed via a post-processing software package developed by the British Antarctic Survey (BAS). The program 'BASTrack' (BAS, v12) was used to decompress the encrypted data downloaded from the logger, providing separate files for light data and temperature recordings. Resulting light data files were loaded into 'TransEdit' (BAS) where times of local sunrise and sunset were estimated from thresholds in the light curves. Threshold values were set at a value of 10 and the 'delete nights < 4 hrs' filter was applied to minimise noise in the transitions. Data were then run in 'BirdTracker' (Bird Tracking CSIDC Project Team, v1.0), where latitude was derived from estimated day length, and longitude from the time of local midday with respect to Greenwich Mean Time and Julian day (Phillips et al. 2004; Fox 2009). This resulted in the calculation of two estimated locations per day per individual bird. The tracking data included in this study were recorded over a one-year period from November 2007 to November 2008.

For the purpose of this study, tracking data during the 'non-breeding' period were extracted from the complete dataset by discriminating it from 'breeding' and 'migration' data based on visualizing the tracks in ArcGIS 9.3.1 (ESRI 2009). This approach was possible due to the predominantly resident behaviour of the birds in the vicinity of their breeding colonies and the straight east-west orientation of migration pathways between breeding and non-breeding grounds, compared to a mainly north-south extent of the non-breeding areas.

Individual arrival and departure dates at or from the non-breeding areas, and hence the duration of respective non-breeding periods, were determined by the point in time when longitudinal movement came to a halt or started again. The extracted track sections for 'non-breeding' were then processed further by eliminating obviously unreliable positions (mainly around equinox when GLS loggers are prone to produce light levels that are uninformative about latitude) and iterative smoothing of the datasets (see Phillips et al. 2004) to account for random deviation of locations. Kernel density estimates were calculated from the filtered GLS locations, using the spatial analyst in ArcGIS 9.3.1 (ESRI 2009). To identify species-specific rather than individual patterns, and also due to latitudinal deviation in the positional data causing considerable distances (>2ºS) between consecutive locations, a search radius of 5 decimal degrees and an output grid size of 0.2 decimal degrees was chosen to visualize the overall spatial distribution as well as core areas at the non-breeding grounds for the three study species. I considered 75% kernel contours more suitable to describe general distribution boundaries than the commonly used 90% or 95%, as some large errors in latitude estimates of the GLS loggers were found using these higher boundaries despite filtering. Core areas were identified via 25% kernel contours.

Movement patterns and sea surface temperature

To identify and describe the spatial and temporal movement patterns of Chatham Albatrosses, Northern Buller's Albatrosses and Northern Royal Albatrosses during the non-breeding period, monthly means of latitude for each species were calculated and plotted over time. Due to small numbers of Northern Royal Albatrosses tracked on either side of the South American landmass (i.e., 5 individuals in Chilean waters and 3 individuals in Argentinean waters), and because this study was focussed on the detection of species-specific patterns, the two groups were combined in subsequent analyses. This approach appeared feasible since both groups occured within very similar latitudinal ranges.

To compare the range of sea surface temperatures (SST) recorded by the GLS loggers between the three study species, daily means of temperature measurements per logger were calculated and then grouped by species. This resulted in 1387, 1983 and 1198 SST values for Chatham Albatrosses, Northern Buller's Albatrosses and Northern Royal Albatrosses, respectively. From these values, monthly mean temperatures were plotted over time to detect potential patterns in the SST ranges frequented by the birds over the course of their respective non-breeding periods. Predominantly sampled temperatures (modal values) were identified

and used as a prompt for further investigations on how respective temperature ranges were distributed over space and time in comparison to the movements of the birds. Based on the location and timing of the non-breeding periods and of each species, monthly composites of remotely sensed SST were downloaded from http://poet.jpl.nasa.gov. These datasets were queried to match the identified modal SST values as recorded by the GLS loggers, and respective ranges were selected for further analysis. Monthly means of latitude from the queried SST distributions were then plotted over time to visualize seasonal changes and check for compliance with or deviation from the spatial and temporal patterns found for each species. Statistical tests were executed within the R software package v2.11.1 (R Development Core Team 2010). Mean values are reported ±SD. In recognition of the latitudinal error in the tracking data, geographic positions are shown as full numbers, since the inclusion of digits was considered as not meaningful in this respect.

RESULTS

The tracking of 15 Chatham Albatrosses resulted in 2458 valid locations (mean latitude = 24 ±10ºS, range 9ºS - 56ºS), while 3413 locations (mean latitude = 22ºS ±8 ºS, range 9ºS - 50ºS) were recorded for 15 Northern Buller's Albatrosses, and 2035 locations (mean latitude = 44ºS ±5 ºS, range 27ºS - 58ºS) were recorded for 8 Northern Royal Albatrosses.

General non-breeding sites and range

All three study species crossed the South Pacific on migration and became sedentary in South American waters. Both Chatham Albatrosses and Northern Buller's Albatrosses stayed along the Chilean and Peruvian coasts, where highest densities were found in areas between 10°S and 20°S, and 10°S and 25°S, respectively (25% kernel, Fig. 1A&B). Overall, Chatham Albatrosses were mainly recorded between 9ºS and 43ºS (75% kernel, Fig. 1A), whereas Northern Buller's Albatrosses showed a more restricted latitudinal range and mostly occurred between 9ºS and 33ºS (75% kernel, Fig. 1B). In contrast, Northern Royal Albatrosses were generally distributed further south than the other two species, with five individuals staying in southern Chilean waters between 34ºS to 49ºS and three individuals staying in the Patagonian Shelf area off Argentina between 36ºS to 54ºS (75% kernels, Fig. 1C). Core areas were identified from 42ºS to 49ºS and 44ºS to 51ºS, respectively (25% kernels, Fig. 1C).

Temporal patterns during non-breeding

There was considerable variation in arrival and departure dates and the time spent in the non-breeding areas, both between species and between individuals within a species. Collectively, Chatham Albatrosses were present off Chile and Peru for 6 months, from February 2008 to July 2008, with individual birds arriving between 25 February and 9 May and departing between 14 May and 26 July. Northern Buller's Albatrosses used their non-breeding areas over 8 months from March 2008 to October 2008, with birds arriving between 19 March and 9 July and departing between 6 August and 27 October. Northern Royal Albatrosses were recorded in either Chilean or Argentinean waters over 10 months from January 2008 through to October 2008, arriving between 22 January and 16 July and departing between 3 July and 17 October. The numbers of individuals arriving at or departing from South American waters per month are given in Table 1. Chatham Albatrosses had a significantly shorter non-breeding period, ranging between 73-116 days (2.5-4.0 months), than either Northern Buller's Albatrosses or Northern Royal Albatrosses which remained within their non-breeding areas for 100-194 days and 91-193 days and (3.0-6.5 months), respectively (Fig. 2; Kruskal-Wallis: $K = 20.5$, $df = 2$, $P < 0.05$).

Movement patterns within non-breeding areas

Despite variability in the individual timing of arrival, departure and duration of residency at the non-breeding areas, distinct species-specific patterns on habitat use during this period could be identified. Comparison by month revealed clear patterns of latitudinal movement over time for both Chatham Albatrosses and Northern Buller's Albatrosses (Fig. 3), with mean monthly distributions shifting northward from the southern end of their range towards high density areas in Peruvian waters, at the northern end of their range.

Chatham Albatrosses present in February and March appeared to stay in southern Chilean waters at mean latitudes of 39 (± 8) ºS and 38 (± 9) ºS, respectively (Fig. 3). Then, between March and May, the mean monthly distributions of the birds shifted north at a rate of about 10 degrees of latitude per month until they came to a halt at mean latitudes of 20 (± 7) ºS (Fig. 3). Thereafter, monthly latitudinal ranges did not change considerably over June and July, when Chatham Albatrosses departed towards their breeding grounds in the Chatham Islands.

Northern Buller's Albatrosses which were present at their non-breeding grounds in March, ranged about 10 degrees further north than Chatham Albatrosses at the time, with a

mean monthly distribution of 30 (± 14) ºS (Fig. 3). Birds remained at similar latitudes in April, where ranges of Northern Buller's Albatrosses largely overlapped those of Chatham Albatrosses. A northward shift in the mean monthly distribution of Northern Buller's Albatrosses was observed between April and June, however at a slower rate. Like Chatham Albatrosses, Northern Buller's Albatrosses stopped proceeding further north in June and July, when their monthly mean distributions remained at 20 (± 7) ºS (Fig. 3). However, birds did not leave from these northern latitudes; instead their mean monthly distribution shifted southwards again over August, September and October when, on average, they departed from latitudes similar to their arrival (Fig. 3).

Monthly mean shifts in the distribution of Northern Royal Albatrosses did not show the same pattern of directed latitudinal movement as found for the other two species. During early stages of their non-breeding period (January – March), Northern Royal Albatrosses were distributed between 50 (± 4) ºS and 47 (± 5) ºS, whereas over subsequent months their mean monthly distribution ranged between 46 (± 4) ºS and 40 (± 5) ºS (Fig. 3). Although the general range apeared to have shifted slightly northwards during April – October, no obvious trend in movement patterns could be detected for this species during that time. To test whether the lack of obvious movement patterns in Northern Royal Albatrosses was due to the comparatively small sample size (N = 8) in combination with individual variation, three different random samples of 8 birds from both Chatham Albatross and Northern Buller's Albatross data sets were extracted and monthly means plotted. The resulting patterns consistently showed the same trend of directional movements as found for the entire sample of the species, suggesting the lack of movement in Northern Royal Albatrosses was not an artefact of small sample size in this species.

Sea surface temperature preferences within non-breeding areas

In situ SST measurements from GLS loggers showed that Northern Royal Albatrosses predominantly frequented cooler waters throughout their non-breeding period than either Chatham Albatrosses or Northern Buller's Albatrosses (Kruskal-Wallis $K = 2576.3$, $df = 2$, $p < 0.05$). SST recordings ranged between 7º-21ºC (median = 11.4ºC) in Northern Royal Albatrosses, 13º-30ºC (median = 18.1ºC) in Chatham Albatrosses and 13º-24ºC (median = 17.5ºC) in Northern Buller's Albatrosses, respectively (Fig. 4). Monthly mean SST values recorded by GLS loggers on Chatham Albatrosses and Northern Buller's Albatrosses changed little over time, ranging between monthly means of 17.1 (± 1.6) ºC and 18.4 (± 1.1)

ºC, and 17.0 (± 0.9) ºC and 18.0 (± 1.1) ºC, respectively (Fig. 5). In comparison, monthly mean SST recordings from Northern Royal Albatrosses showed considerable variation (9.0 ± 1.7 ºC to 14.9 ± 1.9 ºC) over the first months (January – April) of their non-breeding period (Fig. 5). Conversely, throughout May – October, the mean temperature recordings for Northern Royal Albatrosses remained fairly stable in between 10.3 (± 1.8) ºC and 11.8 (± 1.8) ºC (Fig. 5). Whether deviations in the patterns found for Northern Royal Albatrosses were due to small sample size (N = 8) and/or individual variation was tested by investigating as to whether patterns could be detected for the other two study species based on smaller sample sizes. Therefore three different random samples of 8 individual SST recording sets derived from loggers of each Chatham and Northern Buller's Albatross were extracted and monthly means plotted. The resulting patterns consistently showed the same SST preferences as had been found for the entire sample of the two species, confirming they would not change with smaller sample sizes (N = 8). Thus, in theory, a sample size of 8 Northern Royal Albatrosses should have been sufficient to detect clear patterns.

Habitat utilization in relation to sea surface temperature

Overlaying the monthly movement patterns of each albatross species with the distribution of their predominantly used temperature ranges (17º-18ºC for Chatham and Northern Buller's Albatrosses and 10º-12ºC for Northern Royal Albatrosses), revealed spatial as well as temporal congruence (Fig. 6). The mean monthly distributions of the birds moved within approximately the same latitudinal extent as did their respective SST ranges (20º - 40ºS for Chatham Albatrosses and Northern Buller's Albatrosses and 40º - 50ºS in the case of Northern Royal Albatrosses; Fig. 6). Furthermore, the northward movement of Chatham Albatrosses and Northern Buller's Albatrosses coincided with a similar latitudinal northward shift of the 17º-18ºC SST ranges over time, although the birds moved at a slightly faster rate (Fig. 6). However, the mean monthly distribution of Northern Buller's Albatrosses at the end of their non-breeding period (September / October) no longer coincided with the trend in mean monthly latitudes of 17º-18ºC waters, due to birds starting to shift southward again. Nevertheless, Northern Buller's Albatrosses apparently did not entirely leave waters of predominantly 17º-18ºC during these months (see Fig. 5), suggesting that respective SST ranges may have expanded in latitudinal extent while shifting north. In comparison, the cooler temperature ranges (10º-12ºC) predominantly used by Northern Royal Albatrosses during May – October, also shifted northward over the course of the non-breeding season of

this species, although along a smaller latitudinal gradient, between 40º and 50ºS (Fig. 6). Despite the non-linear movement patterns of Northern Royal Albatrosses within this latitudinal range, they likewise appeared to stay within the latitudinal extent matching the distribution of respective temperature ranges (10º-12ºC ,Fig. 6).

Table 1: Number of tracked individuals of albatrosses arriving at and departing from their non-breeding grounds in Chilean and Peruvian waters during January to October 2008.

	Chatham Albatross (n = 15)		Northern Buller's Albatross (n = 15)		Northern Royal Albatross (n = 8)	
	Arrival	Departure	Arrival	Departure	Arrival	Departure
Jan 08					2	
Feb 08	4				2	
Mar 08	8		3		1	
Apr 08	2		2			
May 08	1	1	3		1	
Jun 08		10	6		1	
Jul 08		4	1		1	3
Aug 08				2		1
Sep 08				4		1
Oct 08				9		3

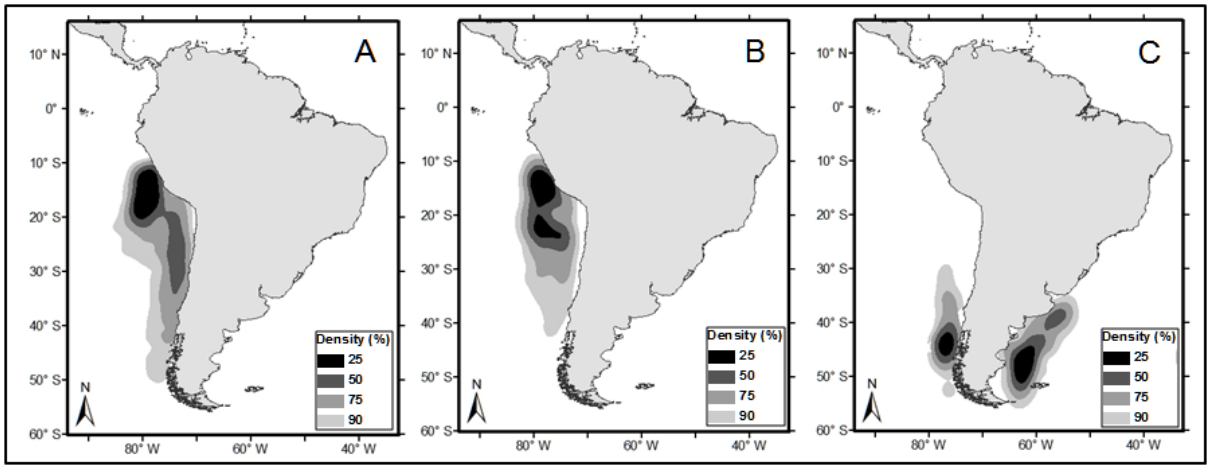

Figure 1: Kernel density estimates of the non-breeding distribution of 15 Chatham Albatrosses (A), 15 Northern Buller's Albatrosses (B) and 8 Northern Royal Albatrosses (C) in South American waters during 2008.

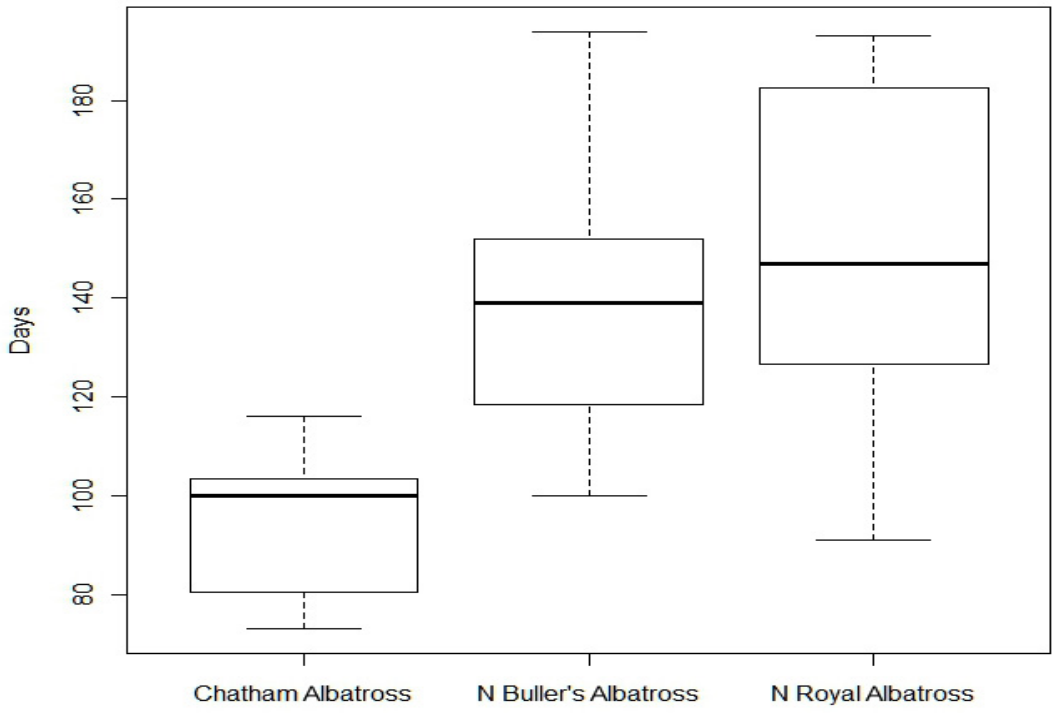

Figure 2: Box plot indicating the duration of the nonbreeding period (in days) of three albatross species tracked in 2008: Chatham Albatross (N=15), Northern Buller's Albatross (N=15) and Northern Royal Albatross (N=8). The figure shows median values, lower and upper quartiles, and minimum and maximum values.

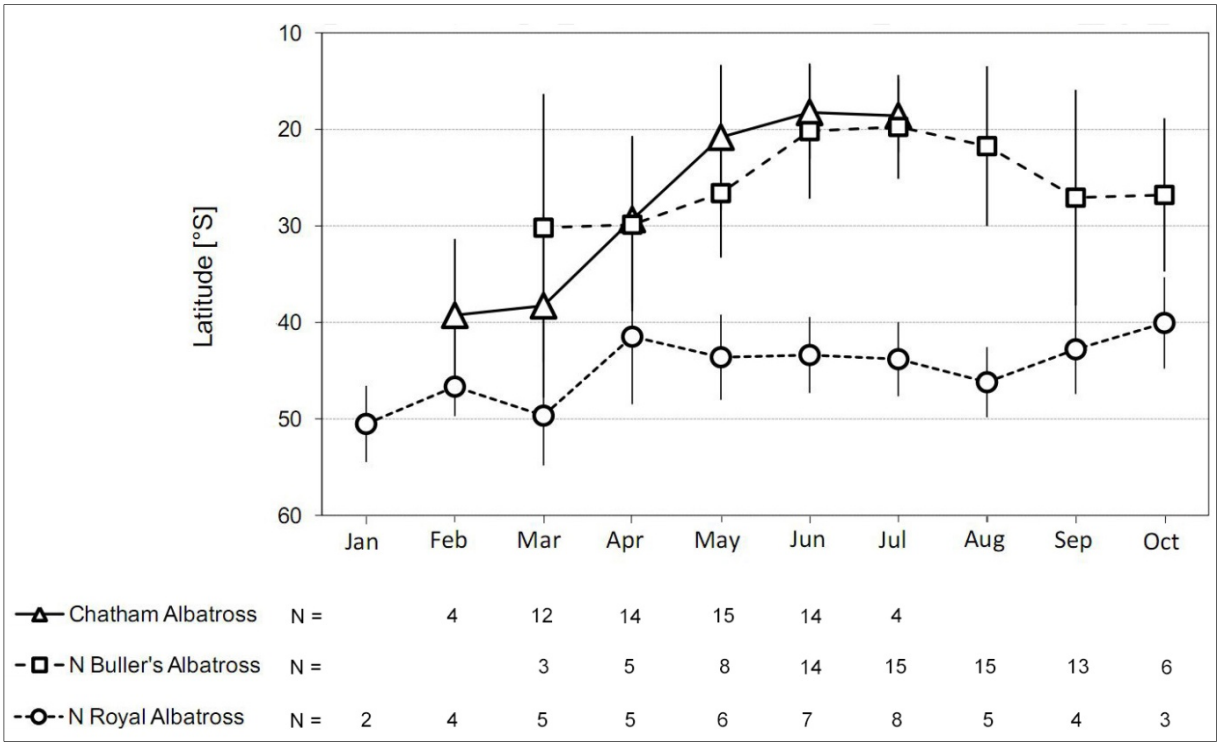

Figure 3: Mean monthly latitudes (±SD) recorded for three species of albatross tracked between January and October 2008. N = number of birds present each month.

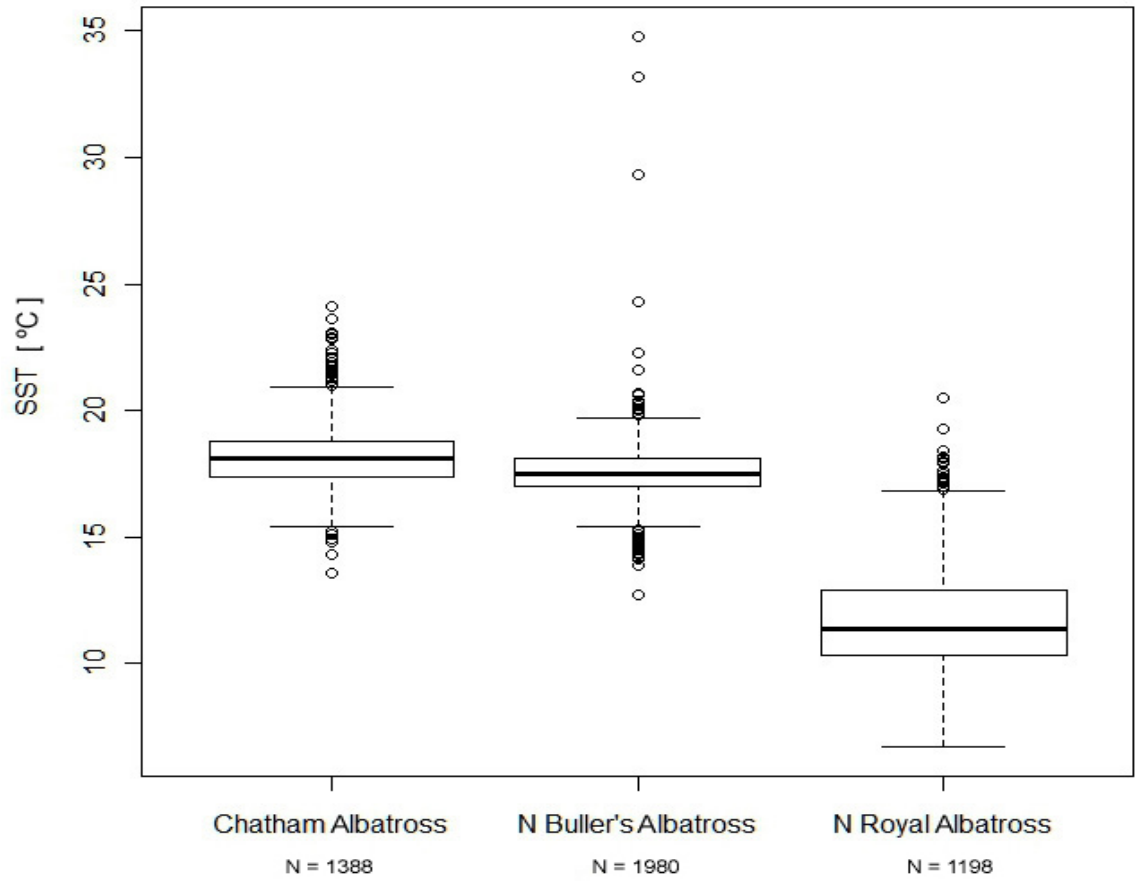

Figure 4: Box plot indicating the range of sea surface temperatures (SST) recorded via GLS loggers on three species of albatross at their non-breeding grounds between January and October 2008. The figure shows median values, lower and upper quartiles, minimum and maximum values, and outliers. N = daily SST values from 15 Chatham Albatrosses, 15 Northern Buller's Albatrosses and 8 Northern Royal Albatrosses.

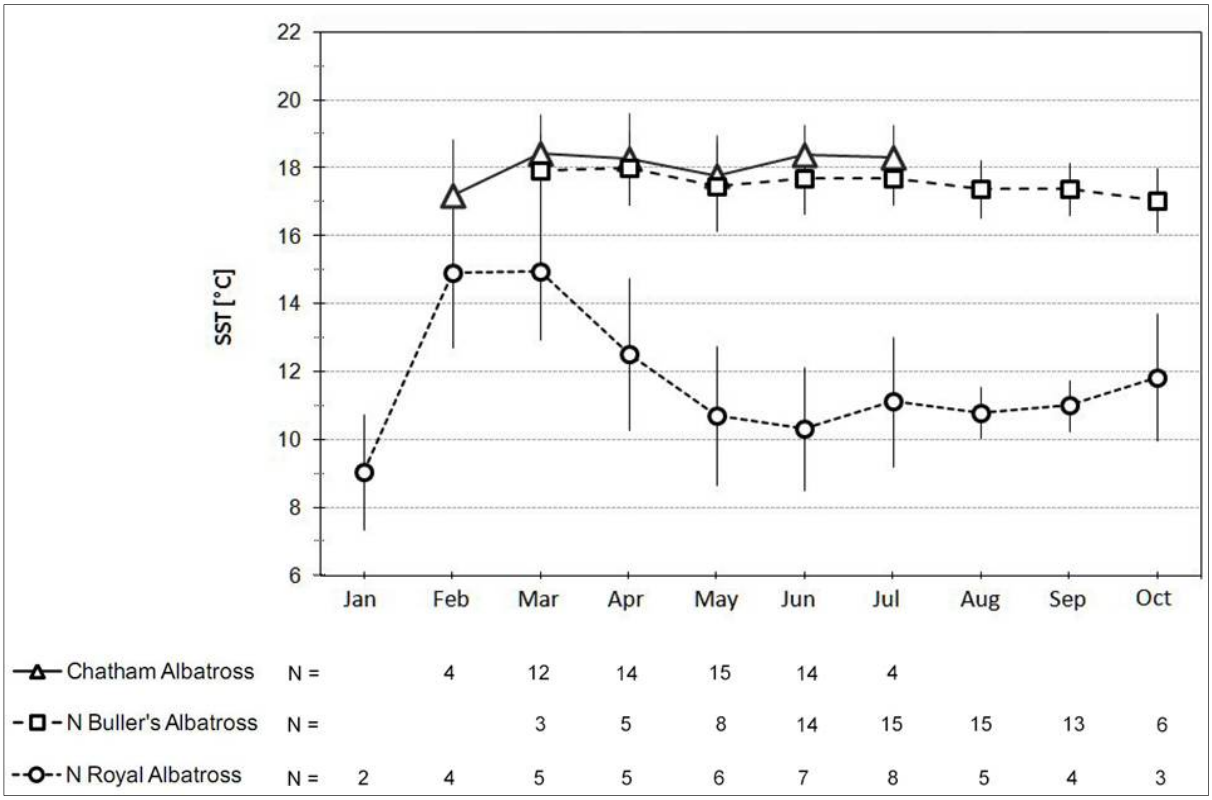

Figure 5: Mean monthly sea surface temperature (daily SST values ±SD) recorded via GLS loggers on three species of albatross at their non-breeding areas between January and October 2008. N = number of birds present each month.

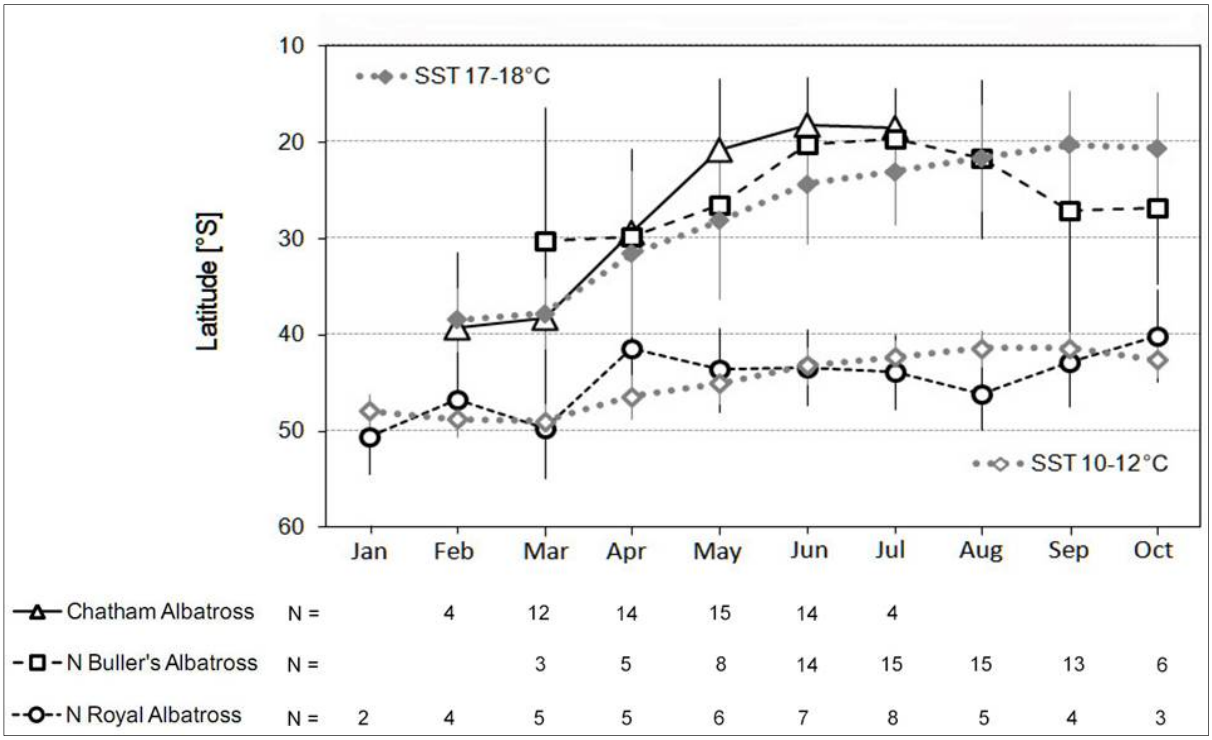

Figure 6: Mean monthly latitudes (±SD) recorded for three species of albatross tracked between January and October 2008 and their predominantly used SST ranges (17-18ºC for Chatham and Northern Buller's Albatross and 10-12ºC for Northern Royal Albatross, respectively). SST values and corresponding spatial information (lat/lon) were derived from remote sensing data sets (http://poet.jpl.nasa.gov). N = number of birds present each month.

DISCUSSION

By using Global Location Sensing (GLS) loggers to track the movements of three species of albatross during their non-breeding period, I identified sea surface temperature (SST) as an important factor related to habitat selection. My results confirmed that Chatham, Northern Buller's and Northern Royal Albatrosses spend the non-breeding season in areas off the coast of South America. In addition I demonstrated that the temporal movement patterns as well as the spatial extent of the non-breeding ranges of the study species was in concordance with the distribution of distinct SST ranges. Moreover, the latitudinal movements of Chatham and Northern Buller's Albatrosses within their respective non-breeding ranges appeared to largely mirror that of latitudinal movements in SST predominantly used by each of the two species. Although no clear pattern could be identified for Northern Royal Albatrosses in this respect, the presented results contribute to a more detailed insight into how these species utilize their marine habitat and how habitat choice is determined over space and time.

The extensive spatial data presented here are consistent with what was observed in previous tracking studies and at sea surveys aiming to describe the non-breeding ranges of Chatham Albatrosses and Northern Royal Albatrosses (Spear et al. 2003; BirdLife International 2004, Nicholls et al. 2005; Nicholls 2007; Nicholls and Robertson 2007; Nicholls et al. 2007). Based on ship-borne observations in Chilean and Peruvian waters, Spear et al. (2003) found Chatham Albatrosses ranged mainly between 13ºS and 41ºS, while satellite tracking studies described the birds as ranging from 7ºS to 40ºS (BirdLife International 2004). The latter matches what was identified as the main non-breeding range for Chatham Albatrosses (9ºS-43ºS) based on 75% kernel distributions in the present study. Moreover, high density areas (25% kernel) at the northern end of the distributional range between 10ºS and 20ºS show extensive overlap with areas described by Nicholls & Robertson (2007), who found Chatham Albatrosses displaying sedentary behaviour from 6ºS to 26ºS off Chile and Peru. For the Northern Royal Albatross, I could confirm that both the east and west coasts of South America are important for this species. The general distributional ranges for Northern Royal Albatrosses from GLS recordings (34ºS to 49ºS off Chile and 36ºS to 54ºS off Argentina) correspond to previous satellite-tracking studies that located the species in Chilean waters between 40ºS and 47ºS and on the Patagonian Shelf between 35ºS and 55ºS (Nicholls et al. 2005; Nicholls 2007). Because of positional inaccuracy in the GLS loggers, differences of a few degrees are more likely due to error than real differences in behaviour of the birds. These results also confirm earlier

suggestions that Chatham Albatrosses and Northern Royal Albatrosses spatially segregate off the South American west coast. It also implies that the use of respective areas is a stable pattern across years for these species.

Prior to this study, no information was available on the non-breeding distribution of Northern Buller's Albatrosses. The few studies on the southern sub-species from the Solander Islands and The Snares (Stahl and Sagar 2000; Sagar et al. 2010), as well as ship-borne observations which did not distinguish between Northern and Southern Buller's Albatrosses (Spear et al. 2003), found non-breeding birds off the Chilean coast between 20ºS and 30-40ºS. The distribution now identified for the Northern Buller's Albatrosses via GLS logging, ranging from 9ºS to 33ºS (75% kernel) along the South American west coast, poses the question whether the northern subspecies might venture further north into Peruvian waters than the southern subspecies. However, such suggestions will need to be backed up by more data on the distribution of both subspecies. The non-breeding range of Northern Buller's Albatrosses completely overlapped with the one identified for Chatham Albatrosses, but was more restricted in its southern extent, and thus segregated more clearly from the southerly ranges of Northern Royal Albatrosses off the Chilean coast. This is probably attributable to the SST ranges tracked by Northern Buller's Albatrosses having moved already further north by the time this species arrived, which was about a month later compared to Chatham Albatrosses.

Timing and duration of non-breeding

Robertson and Nicholls in BirdLife International (2004) reported satellite-tracked Chatham Albatrosses in Chilean waters from January to April, which is similar to the current study in which I found birds arriving in February and leaving by May. The arrival times recorded for Northern Royal Albatrosses in my study (from January to March and again between May and July) also support, at least in part, earlier satellite-tracking studies that describe birds arriving in Chilean and Argentinean waters between January and March (Nicholls et al. 2002). They reported birds to spend 103-198 days in their respective areas, with closely matches my findings of non-breeding durations for Northern Royal Albatrosses of 91-193 days. Inter- and intra-specific variation in the timing and duration of the non-breeding period is likely to be influenced by both species-specific as well as individual breeding schedules and behavioural patterns. It is also possible that the timing and duration of non-breeding movements depend on whether a bird bred successfully or failed.

Albatross distribution and SST

In situ measurements via the GLS loggers identified 17º-18ºC waters as predominantly frequented by Chatham and Northern Buller's Albatrosses throughout their stay in South American waters. Spear et al. (2003) associated Chatham Albatrosses with waters around 19ºC and Buller's Albatrosses (no sub-species distinguished) with waters around 16ºC, based on measurements in the vicinity of bird sightings over the course of 15 boat cruises between 1980 and 1995 off the Chilean and Peruvian coast. Their observations were conducted during the austral autumn and winter (March – July), equivalent to the period in which Chatham Albatrosses were recorded in the present study. Although not an exact match, the results of both studies point towards temperate waters being primarily favoured by these species. It is likely that a certain amount of birds recorded as only 'Buller's Albatross' might belong to the southern subspecies, which could explain differences in observed SST ranges, although annual variability in environmental conditions could also be a likely cause. The association of Chatham Albatrosses with temperate waters within their non-breeding area appears to be slightly more consistent over time.

The non-breeding areas of both Chatham and Northern Buller's Albatrosses are dominated by the Humboldt Current System (HCS), which begins where South Pacific temperate waters meet the Chilean coast between 40ºS and 50ºS and transports cool and nutrient-rich waters northwards along the South American west coast to about 5ºS, where currents change direction and proceed northwest to the Galapagos Islands (Spear et al. 2003; Thiel et al. 2007). The present study shows that within this oceanic current system, the two species are not randomly distributed, as in being spread out across their whole non-breeding range at all times, but follow the northward shift of waters of their preferred SST range over time. It has to be noted, however, that the shift in water temperatures as shown in this chapter is a seasonal event and is not generally linked to the movement and directions of currents at all times.

The link I identified in this study between the distribution and movements of albatrosses and SST might explain why Chatham Albatrosses and Northern Buller's Albatrosses differ in the southern extent of their non-breeding areas. Birds arriving off the Chilean coast earlier in the season start further south in concordance with the distribution of 17º-18ºC waters, which ranged around 40ºS in February and March, a time when Chatham Albatrosses arrived in Chilean waters at mean latitudes of also about 40ºS. Respective temperature ranges had shifted to around 30ºS over the course of April and May, when more Northern Buller's

Albatrosses reached their non-breeding grounds. Thereafter, the monthly distributions of the two species largely overlapped while moving north and arriving at the northern end of their range. The fact that Northern Buller's Albatrosses moved south again while remaining within their preferred SST range (as shown by the GLS temperature recordings), suggests that the latitudinal extent of 17º-18ºC waters broadened once they reached their northern limit. This increase in latitudinal range of temperate waters might be induced by the Peru-Chile Counter Current within the HCS (Thiel et al. 2007), which causes a slight southward drift in the current until it reaches about 35ºS, 100-300 km off the coast.

In comparison to Chatham Albatrosses and Northern Buller's Albatrosses, waters predominantly used by Northern Royal Albatrosses during their non-breeding period were colder, ranging from 10º-12ºC. Water of this temperature, on average, does not reach further north than 40°S during the non-breeding season of Northern Royal Albatrosses (January – October), approximating the mean distributional range of the species on both sides of the South American continent. Northern Royal Albatrosses did not show clear and linear movement patterns like the other two study species. The assumption that this may be due to a small sample size where individual variation may prevent detecting clear patterns in their non-breeding behaviour does not appear to be the explanation since distributional patterns were clearly evident for the other two study species (Chatham and Northern Buller's Albatross) even when smaller sample sizes were investigated. However, there might be a higher degree of individuality inherent in Northern Royal Albatrosses (considering they occupy two non-breeding sites at the same time and it is to date not clear why that is so) and larger sample sizes might be needed to reliably confirm or deny the existence of species specific patterns during non-breeding. It appears though, that during the early months in the non-breeding period (January – April) of Northern Royal Albatrosses, warmer water masses were still present in the northern parts of their distributional range and thus temperatures above 10º-12ºC could prevail due to birds not necessarily moving north, but starting out at higher latitudes and corresponding SST at the time. The later northward shift of cooler waters may then reduce individual variation at a later stage, when 10º-12ºC waters occupy most of the birds distributional range (May – October).

In Argentinean waters, Northern Royal Albatrosses were found across the entire Patagonian Shelf, an area in which the Malvinas Current transports cold and nutrient rich waters northwards along the shelf edge between 55°S and 38°S, where it collides with the warm waters of the Brazil Current (Matano et al. 2010; Piola et al. 2010). This confluence

zone creates thermal and saline gradients and leads to the formation of productive fronts in the north (Falabella et al. 2009). Since Northern Royal Albatrosses spent most of their time to the south of this region (according to core areas identified by kernel analysis), I suggest this may well be due to a preference for colder waters, despite more individual variability than observed for the other species. This interpretation is supported by the observation that individuals of Northern Royal Albatross which frequented waters off southern Chile, in an area where the HCS starts its northward drift, did not follow the movement of temperate waters along the prevailing currents like Chatham and Northern Buller's Albatrosses, but remained within the ranges of 10°-12°C. This again suggests active habitat selection by the birds in response to SST and any changes in prey availability to which it is associated. This also indicates that the identified patterns of spatial segregation of the three species in their non-breeding areas may be associated with SST.

My findings agree with several studies that have found other species of Procellariiformes segregating at their non-breeding sites based on SST but also ocean productivity (Phillips et al. 2006; Bugoni et al. 2008; Kappes et al. 2010; Rayner et al. 2011). The two species which did spatially overlap in my study (Chatham and Northern Buller's Albatross) showed temporal segregation to a certain degree, with the majority of Northern Buller's Albatrosses arriving later and staying longer. This could be due to differences in breeding schedule and pre-breeding behaviour of the two species and might serve the reduction of inter-specific competition.

SST and other environmental factors

Bathymetry has been considered an important factor explaining the non-breeding distribution of albatrosses in South American waters. Satellite-tracking studies (BirdLife International 2004) found Chatham Albatrosses being confined to a narrow band along the steep continental shelf slope between 500-5000 m off the coasts of Chile and Peru. Based on ship-borne observations throughout the HCS, Spear et al. (2003) found Chatham Albatrosses frequented more offshore waters than Buller's Albatrosses (no sub-species distinguished) which instead preferred the continental slope. However, Chatham Albatrosses were seen foraging significantly more often over the continental slope than in pelagic waters. Satellite-tracked Northern Royal Albatrosses were likewise found largely over the continental shelf and slope areas in both Chilean and Argentinean waters (Nicholls et al. 2005; Nicholls et al.

2007). In a comparative study, they were found to segregate from two other *Diomedea* species, which frequented deeper oceanic waters (Nicholls et al. 2002).

Due to its temporally flexible nature, SST appears to be more informative when it comes to identifying areas of importance for albatrosses on both temporal and spatial scales, compared to a static factor like bathymetry. In any case, understanding the cues and processes that birds use to move and navigate within their general non-breeding areas can be a valuable when studying the drivers of habitat use. According to my results, SST appears to be at least a highly influential factor for albatross distribution within the Humboldt current system. The importance of SST is supported by Spear et al. (2003), who also identified SST as the major factor for habitat selection of Chatham and Buller's Albatrosses based on a principal component analysis of five different marine habitat parameters (SST, salinity, thermocline depth and strength, and wind speed). Nevertheless, my results do not explain why both Chatham and Northern Buller's Albatrosses occurred in highest densities at the northern end of their non-breeding range since their SST preference remained unchanged over time. Thus, while SST appears to be a major variable in explaining movements within the non-breeding habitat, other environmental factors have to be taken into account to explain why the birds yet again concentrate in certain places. The high densities of Chatham and Northern Buller's Albatrosses (mostly recorded in Peruvian waters), while still within their preferred SST range, are also located in a region of highly productive coastal upwelling (Carr 2001). Spear et al. (2003) described maximum upwelling in this area during the austral winter, which matches the period (May - August) in which Chatham Albatrosses and Northern Buller's Albatrosses were recorded in this area during the present study, indicating productivity may be a factor which affects concentrations of birds within a particular band of SST.

All three species of albatross in my study are opportunistic predators, since their diet ranges from small items like Euphausiids to large salps, squid and fish (ACAP 2009a, b, c). In the HCS, anchovy (*Engraulis ringens*) is thought to be the most important fish species and the major prey of top predators (Espinoza and Bertrand 2008). These fish were found associated with water off the coast of Peru (i.e., high density areas of Chatham Albatrosses and Northern Buller's Albatrosses) that are characterized by temperatures ranging between 14°-19°C (Swartzman et al. 2008). One of the major spawning areas of the anchovy is also located off southern Peru and stretches through to 25°S (Acha et al. 2004), where reproduction peaks during the austral winter (Castro et al. 2000). Furthermore, the distributional range of the anchovy from 4°S through to 42°S approximately matches the

general extent of the HCS as well as the range of Chatham Albatrosses and their preferred SST (17-18°C). The continental shelf break and inner slope of the southern Chilean and Argentinean non-breeding sites of Northern Royal Albatrosses have been found to be distributional centres of one of their preferred food species during the breeding season, the cephalopod *Morotheuthis ingens*, which has been suggested to be a possible explanation for the selection of this habitat by the birds during non-breeding (Imber 1999; ACAP 2009c). *M. ingens* has been described to occur in cooler sub-Antarctic and Antarctic intermediate water masses (Jackson et al. 2000). Unfortunately little has been published on what causes fish distribution in the study area. Whether the SST preference of Chatham Albatrosses, Northern Buller's Albatrosses and Northern Royal Albatrosses is due to the targeting of different prey species requires future research.

Conclusion

Despite limitations in precision, my results illustrate that GLS tracking data in combination with *in situ* SST measurements and remote sensing data can be a useful tool to identify and characterize important marine areas for albatrosses at sea on a reasonably detailed spatial and temporal scale. I could provide evidence that SST is an important factor in the habitat selection of three different albatross species during their non-breeding period by showing how this factor correlates with their movement patterns within the non-breeding ranges on a monthly basis. The present study confirms the importance of both the western and eastern coasts of South America for New Zealand albatrosses, where they are likely to interact with human activities like commercial fisheries along most of their range. A better understanding of the spatial and temporal patterns of albatross species using this area will be crucial for ensuring useful management of fisheries and other activities that have the potential to affect albatross survival.

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CHAPTER 3

Migration routes and stopover behaviour in the Chatham Albatross

ABSTRACT

The strategies by which Procellariiform seabirds exploit the marine environment on migration vary widely. Using geolocation devices with integrated saltwater immersion sensors, I studied the migratory patterns of the endangered Chatham Albatross (*Thalassarche eremita*) over three consecutive years (2008-2010). Migration routes were highly consistent with birds crossing the South Pacific at the same mean latitude of 40°S each year when commuting between their breeding site in the Chatham Islands and non-breeding grounds in South American waters. Despite individual variation, the general timing of migration on species level remained similar over the three years, with peaks in migratory activity during March/April (post-breeding) and June/July (pre-breeding). Likewise, the level of variance in the duration of migration (7-36 days) proved to be consistent in the population across years. Most birds made stopovers on both post- and pre-breeding migration and these varied from 3 to 26 days in duration, although not every individual engaged in stopover behaviour. As one might expect, the duration of migration correlated positively with the duration of stopovers, but was also subject to individual as well as variation due to the direction of migration (post- or pre-breeding) and year. When on a stopover, Chatham Albatrosses spent more time on the water during both day and night, and displayed an increased degree of alternating between landings and take-offs during the day. The high number of alternations between landing and take-off observed for Chatham Albatrosses on migration suggests this species actively forages while en route and that the birds follow an "energy selective" rather than a "time selective" migration strategy. My findings stress the importance of the South Pacific high seas and the Subtropic Frontal System as potential foraging habitat for Chatham Albatrosses while on migration, and highlight the need to consider these regions when developing a comprehensive annual network of important marine areas for New Zealand albatrosses. The dynamic pattern in the use of the high seas environment and its resources by migrating albatrosses suggests that conservation measures need to focus more on the mitigation of potential threats throughout their range rather than designation of actual boundaries of protected areas.

Key words: Albatrosses, migration, stopover, activity patterns, Chatham Islands

INTRODUCTION

Migration is any movement caused by temporal and spatial changes in habitat quality and is common in species populating higher latitudes where food availability varies seasonally (Alerstam et al. 2003; Mackley et al. 2010; Pinet et al. 2011). Time minimisation is hypothesised to be paramount in migration strategy, but the minimisation of energy costs also plays an important role in shaping migratory patterns (Hedenström 2008). The timing of migration is of particular importance in the ability of animals to exploit seasonal habitats and reduce inter-specific competition (Croxall et al. 2005). Dingle and Drake (2007) recognise two types of migration: 1) 'to-and-fro' migration, describing the commute between two destinations along the same route, and 2) 'roundtrip' migration, where birds follow different paths on the outward and return journeys and/or stage their movements through a succession of non-breeding areas between two breeding seasons. Similar to the latter, migrants may switch between migration and foraging while en route, termed as stopovers (Dingle and Drake 2007). Such behaviour is common in long-distance migration where the commute between widely separated areas is divided between cycles of energy accumulation and movement toward the final destination (Akesson and Hedenström 2007). Dividing travel times into shorter episodes which can be covered with smaller fuel reserves is thought to minimise the energy costs of migration (Alerstam et al. 2003). Stopover sites can be traditional locations where individuals aggregate in the same areas over consecutive migration periods and years (Egevang et al. 2010; Kopp et al. 2011), but stopovers can also be temporary and spatially flexible, when birds follow the 'fly-and-forage migration strategy' (Klaassen et al. 2012).

For marine predators like seabirds, migration can be driven by oceanic processes, species-specific thermal tolerances and shifts in prey distributions (Block et al. 2011). In some species, oceanic currents and winds may be exploited to facilitate migration, and such environmental features have the potential to even influence the evolution of certain migration routes (Alerstam et al. 2003). Recent studies have shown wind to be a major determinant of the migratory routes of seabirds, defining spatiotemporal pathways as well as barriers for large-scale movements, often resulting in the migration of seabirds not necessarily following the shortest route but so-called low-cost ''wind-highways'' (Felicísimo et al. 2008; Gonzalez-Solis et al. 2009). Procellariiformes (e.g., petrels, albatrosses, and relatives) depend largely on wind and wave energy for efficient flight (Adams and Flora 2010). Dispersal strategies in this order range from resident to partially and highly migratory (Mackley et al. 2010). While

for some species the migratory journey is just a continuation of their inherently wide-ranging lifestyle (Hodum 2006), others are long-distance migrants, integrating one or several distinct non-breeding destinations on their travel across or around whole ocean basins (Phillips et al. 2005; Shaffer et al. 2006; Suryan et al. 2007; Felicísimo et al. 2008; Rayner et al. 2011). Thus, there is no common pattern according to which the marine environment is utilized by pelagic birds on migration, as we find all the migration strategies described by Dingle and Drake (2007) adopted by this group. Different migration strategies sometimes even show within the same species (Croxall et al. 2005; Suryan et al. 2006). While many species appear to be consistent in their migration strategies, such patterns are not fixed from one year to the next and can change rapidly when conditions alter (Phillips et al. 2005; Kopp et al. 2011). At-sea activity patterns on migration remain poorly understood, particularly for pelagic species like albatrosses and petrels (Mackley et al. 2010; Stenhouse et al. 2012). Knowledge of the movements and behaviour of these species during the non-breeding period, and of the spatial use of marine habitats during that time, can add considerably to our understanding of marine ecosystem dynamics (Stenhouse et al. 2012). Stopover sites and patterns on migration should play an important role in this respect but due to the highly mobile nature of migrants, the role of these patterns in marine dynamics often remain unrecognized (Guilford et al. 2009).

The current study investigates the migratory patterns in the Chatham Albatross (*Thalassarche eremita*), a species endemic to New Zealand and listed as 'endangered' by the IUCN (www.iucnredlist.org, version 2011.1). Birds exclusively breed in the Chatham Islands and spend most of their non-breeding period off the coast of Chile and Peru (Spear et al. 2003; BirdLife International 2004; but also see Chapter 2). Accordingly, individuals have to cross the South Pacific ocean on their commute between the two sites. It is assumed most albatross species cannot sustain long-distance flight over consecutive days without substantial periods of rest (Mackley et al. 2010), and hence alternate periods of flight with periods on the water (Weimerskirch and Wilson 1992; Viswanathan et al. 1996; BirdLife International 2004). However, when in flight, albatrosses are amongst the fastest travellers due to their ability to utilise dynamic soaring by exploiting vertical wind speed gradients (Alerstam et al. 2003; Akesson and Hedenström 2007), and it has been shown that rapid non-stop flight can be sustained for up to 9 hours in association with high tailwinds (Catry et al. 2004). Records of Grey-headed Albatross (*Thalassarche chrysostoma*) circumnavigating the globe on migration in just 46 days (Croxall et al. 2005) are certainly proof of at least some species being capable of extremely rapid migration. For the Chatham Albatross, Nicholls and

Robertson (2007) reported "rapid and consistent change in longitude eastwards from 170°W to east of 80°W" when describing the movements of three individuals tracked with satellite transmitters (PTT) during post-breeding migration in 1997 and 1998. Yet, the same authors (in BirdLife International 2004) described the duration of post-breeding migration to vary between 11 and 30 days, based on a total of 10 Chatham Albatrosses tracked via PTT during the 1990's. They also noted "areas of concentration" within the central Pacific, and considered that becalming weather conditions may have caused interruptions in migratory movements.

Apart from these records, which only covered post-breeding migration, nothing is known about how Chatham Albatrosses utilise the marine environment they traverse on migration. Indications are that individuals interrupt their migration, but it is not clear whether such interruptions can be categorized as stopovers, and if so, whether stopovers are a common or consistent pattern in the species and what their function may be in the case of the Chatham Albatross. Thus, given the current fragmentary nature of our understanding of the migration strategies found in Chatham Albatrosses, the objective of this study was to use geolocation devices (GLS) to record the annual movements of the birds over consecutive years to gather comprehensive information on the whole migratory cycle of the species. Specifically, I quantified: (1) the course, timing and duration of post-breeding and pre-breeding migration of Chatham Albatrosses, and (2) the stopover behaviour of birds while on migration.

METHODS

Study site and study species

Chatham Albatrosses were studied on The Pyramid (44°25'S, 176°14'W) in the Chatham Islands, New Zealand. This location is the world's only breeding site for the species and holds an estimated 4,600 annual breeding pairs (ACAP 2009a). They are listed as 'endangered' by the IUCN (www.iucnredlist.org, version 2011.1.) and as 'naturally uncommon' in recent New Zealand threat rankings (Miskelly et al. 2008). They have been identified as a species requiring monitoring and research in the New Zealand National Plan of Action (NPOA-Seabirds; Taylor 2000) and also in recovery plans for albatrosses in the Chatham Islands (Department of Conservation 2001, 2004).

Logger deployment and data processing

To record the movements and times of migration of Chatham Albatrosses, Global Location Sensing (GLS) loggers were fitted to a total of 52 individuals whilst breeding in November/December 2007, 2008 and 2009. The devices (GLS-Mk5, 18 x 18 x 6.5 mm, 3.5 g, battery life ~ 6 years) were built by the British Antarctic Survey (BAS) and set to record date, time, light intensity and immersion in seawater. The GLS loggers were attached to plastic leg rings, using "liquid nails" glue and steel-reinforced cable ties, and then placed on the tarsi of the selected birds while they were either incubating or chick rearing. The total weight of the attachment was 7 g, corresponding to about 0.1 - 0.2 % of the average body mass of each species, and hence below the recommended threshold of 3 %, above which adverse behavioural effects can be expected (Phillips et al. 2003). All birds were also fitted with a numbered metal ring and their nest sites were mapped and marked for re-identification and to allow recapture of returning birds over subsequent years. To ensure optimal retrieval rates, only adult breeding birds were chosen for this study, as they were more likely to be recovered at the same nest location than non-breeding adults or immature/prospecting birds.

Overall, tracking data could be retrieved from 45 individuals. For 6 individuals, data were collected in all three years addressed in this study (2008, 2009 and 2010), while 20 individuals were tracked over two consecutive years (8 during 2008 and 2009 and 12 during 2009 and 2010), and 19 individuals were tracked during just one year (2 in 2008, 6 in 2009 and 11 in 2010). This resulted in a total of 77 annual tracks, of which two were missing data during pre-breeding migration due to battery failure of the logger. The tracking data were analysed using post-processing software packages developed by the British Antarctic Survey. Logging files were decompressed using 'BASTrack' (BAS, v12), providing separate files for light and saltwater immersion recordings. Light data files (i.e., values ranging from 0 – 64, resulting from the measurement of light levels every 60 s logged as the maximum value over each 10 min recording interval) were loaded into 'TransEdit' (BAS) where times of local sunrise and sunset were estimated from thresholds in the light curves. Threshold values were set at a value of 10 and the 'delete nights < 4 hrs' filter was applied to minimise noise in the transitions. Sunset and sunrise times were used to subsequently calculate latitude via the estimated day length, and longitude via the time of local midday with respect to Greenwich Mean Time and Julian day (Phillips et al. 2004; Fox 2009) in 'BirdTracker' (Bird Tracking CSIDC Project Team, v1.0), resulting in two estimated locations per day. Obviously unreliable positions (mainly around equinox when day and night length were equal and thus

algorithms estimating position were inaccurate) were eliminated and iterative smoothing of the datasets (see Phillips et al. 2004) was applied to account for random deviation of locations.

Track data

To visualise the overall spatial distribution of Chatham Albatrosses throughout the study period and to describe migration pathways, locations were plotted in ArcGIS 9.3.1 (ESRI 2009) and kernel density estimates were calculated using the spatial analyst with a search radius of 5 decimal degrees and an output grid size of 0.2 decimal degrees (WGS 1984). The comparatively large search radius was chosen to identify species-specific rather than individual patterns, and to account for the considerable latitudinal deviation in the positional data, which was especially pronounced around equinoxes but also appeared to be stronger during periods of fast movement. Each annual bird track was categorised into 'breeding', 'migration', and 'non-breeding' sections, where 'migration' described the period when birds were commuting between areas of prolonged residency, i.e. crossing the South Pacific between breeding area (Chatham Islands) and non-breeding grounds (Chile and Peru). The 'migration' sections were then selected for further analyses. Migration dates were identified by visual inspection in ArcGIS 9.3.1 (ESRI 2009) as the start- and end points of progressive east- (post-breeding) or westbound (pre-breeding) longitudinal movement. Based on this information the duration of migration was calculated as the number of days a bird spent between departing the breeding area and arriving at the non-breeding grounds (= 'post-breeding migration') and vice versa (= 'pre-breeding migration'). The migration tracks were divided into legs of 'continuous migration' and 'stopovers'. Stopover events were identified via track patterns which indicated 'resident' behaviour (i.e., no or little longitudinal movement or repeated change of direction like zigzag or loop patterns) over the course of a minimum of three consecutive days. Periods shorter than three days were considered unreliable to detect such patterns, due to the general spatial imprecision in the actual GLS tracking data sets, combined with the fact that no more than a maximum of two positions per day were available. This approach was similar to that in a recent study by Hedd et al. (2012), where a threshold of >2 days was set when identifying stopovers within GLS tracks of Sooty Shearwaters (*Puffinus griseus*). The duration of stopovers was calculated as the number of consecutive days during which 'resident' behaviour occurred. Locations of stopovers along each of the bird's migration pathways were described as mean values of respective latitudes and longitudes to account for often comparatively high inaccuracies in the latitudes of

migration tracks. Those inaccuracies presumably resulted from birds tucking their feet under their undertail-coverts when flying (personal observation), causing intermittent shading during the day, and also because the main post-breeding migration took place around equinox.

Activity data

Activity patterns of Chatham Albatrosses were analysed based on immersion recordings of the GLS loggers which provide time-budget data related to the bird's activity (Afanasyev 2004). Loggers tested for saltwater immersion every 3 s and logged the number of positive tests within each 10 min recording interval, resulting in values from 0 (always dry) to 200 (always wet; Fox 2009). Corresponding values were categorised into three distinct states of activity: 'sitting on water' (or activity state = 'wet') when the logger was continuously immersed during a 10 min recording interval, 'in flight' (or activity state = 'dry') when the logger recorded no immersion during a 10 min recording interval, and 'alternating between landing and take-off' (or activity state = 'mix') when immersion values ranged from > 0 to < 200, indicating that the bird did change between activity states 'wet' and 'dry' at least once within a 10 min period. Since the objective was to address whether stopovers corresponded with changes in the bird's activity and, furthermore, if activity patterns indicate an increase in potential foraging behaviour, only 'on water' and 'landing/take-off' activity were included in further analysis. This was based on the assumption that a bird sitting on the water for > 10 min was either resting or feeding, while alternating between landings and take-offs over at least a 10 min period was likely to reflect either more actively foraging within a certain area or that the bird was commuting between potential foraging locations. To quantify activity states, the count of respective 'events' (= 10 min intervals of 'wet' or 'mix' recordings) was calculated as a percentage of the total number of activity events recorded, corresponding with the proportion of time spent at either activity state during a defined period like day or night, stopovers or continuous migration, post- or pre-breeding migration, and/or different years. Information on day and night (i.e., light and dark periods) was derived from the estimated transition times for start/end of civil twilight calculated by the 'TransEdit' software (BAS), based on sun elevation angles of -4 degree, during the processing of light data files from the GLS loggers. Respective information could not be discerned from raw light data files, since the occurrence of 'artificial nights', i.e. dark periods due to shading events during daytime were common. Such shading events were only observed when the bird was in flight, thus a likely cause is that the bird had tucked its feet underneath the feathers.

Statistical analysis

For the analysis of the duration of migration, data from all tracked individuals (n = 45) were used, whereas for the analysis of activity patterns only data sets from individuals which actually made stopovers on migration (n = 36) were selected, since the main focus here was on comparing activities during sections of continuous migration and stopovers. Data values are presented as mean ±SE.

To explain the variance in the duration of migration of Chatham Albatrosses as well as variance in the measured proportions of time spent in a certain activity state ('wet' = proportion of time spent on water, and 'mix' = proportion of time spent alternating between landing and take-off), general linear mixed effects models (glmm) were fitted to the respective data sets, using Gaussian (for duration data) and binomial (for activity data) response models with corresponding identity and logit link functions. This model structure was applied because GLMMs allow for both fixed and random effects to be incorporated in the model, and thus account for non-independence of data sets resulting from individuals being tracked over multiple years by permitting the intercept parameter to vary randomly across individuals. For this reason bird ID was included as a random effect in all models. For the response variable 'duration of migration' (number of days) the following explanatory variables were included as fixed effects: 'year' (2008/2009/2010), 'migration direction' (post-/pre-breeding), 'stopover event' (yes/no) and 'stopover duration' (number of days). Similarly, in models explaining activity states ('wet' or 'mix'), 'year' and 'migration direction' were also included as fixed effects into the models, together with 'migration status' (continuous migration/stopover), and 'time of day' (light/dark period).

To analyse the effect of the respective explanatory variables on the characteristics of the response (migration duration or activity), multi-model inference was made using the Information-Theoretic Model Comparison (ITMC), addressing multiple alternative hypotheses in a set of *a priori* candidate models. This approach is recommended for making formal model inferences and can provide more meaningful model likelihoods and probabilities using Akaike's Information Criteria, AIC (Anderson 2008) when comparing the ability of different models to explain variation in the investigated response. Sets of 25 (for duration of migration) and 27 (for either activity state 'wet' or 'mix') candidate models were used to test for the effects of individual variation only (i.e. 'null model', with only random factor ID), of single explanatory factors and combinations as well as interactions thereof, including 'global models' (all explanatory variables). All models were fit using maximum

likelihood estimation within the framework of the statistical programme R (R Development Core Team, 2010), applying packages 'lme4' (Bates et al. 2011) and 'AICcmodavg' (Mazerolle 2012). Model inference was based on Akaike's Information Criteria (AICc was used to correct for second order bias, accounting for small sample sizes; Mazerolle 2004). AICc penalizes for each additional factor included into the model, selecting for the most simple and parsimonious model (Mazerolle 2004). Log likelihoods and AICc values were calculated and each model was ranked by rescaling the AICc values. Best model fit was indicated by comparatively high likelihood and small AICc values, providing a formal strength of evidence for each of the models (Burnham et al. 2011). The expected distance between the best model and the $_i^{th}$ model was described by $\Delta_i = \text{AICc}_i - \text{AICc}_{min}$. Models with $\Delta_i \leq 2$ can be considered to have substantial support; models with $\Delta_i < 7$ have some empirical support, while those with $\Delta_i \geq$ 10-12 essentially have no empirical support (Burnham and Anderson 2002). Akaike weights (W_i) were used to examine the relative strength of evidence for each model within the set, indicating the probability for model *i* being the best model (Mazerolle 2004). Additionally, cumulative Akaike weights (Cum.w_i) was called on as a measure of confidence in the top ranking models to best explain the observed variance of the response variable.

RESULTS

Migration route

The 45 individuals of Chatham Albatross tracked in this study were consistent in their selection of migration routes. In all three years (2008, 2009 and 2010) the birds crossed the South Pacific at the same mean latitude of 40°S (±0.3, ±0.2 and ±0.2, respectively) on their migration between breeding grounds in the Chatham Islands and non-breeding grounds off the west coast of South America. The latitudinal extent of the area frequented on migration (30–50°S, based on 95 % kernel densities) also remained the same between years, and followed the approximate course of the Subtropical Front (Figure 1).

Timing and duration of migration

Departure and arrival dates

Considerable individual variation was found in the departure and arrival dates for both post- and pre-breeding migration of Chatham Albatrosses (see Appendix 1 for individual migration

dates). During 2008-2010, birds left their breeding grounds between late January and early April, and arrived at their South American non-breeding sites between early February and early May (Table 1). Return migration commenced between mid May and early August and birds arrived at their breeding grounds within the same time window between late May and mid August (Table 1). Variation in departure and arrival dates remained similar each year. Migratory activity peaked in February and March (post-breeding) and June and July (pre-breeding; Figure 2). On pre-breeding migration the same proportion of birds migrated during the two peak months in all years. On post-breeding migration however, more birds migrated during March than February in 2008, while it was the other way round in 2009 and 2010 with more birds migrating in February than March. This was also evident in the mean departure and arrival dates which were earlier in 2009 and 2010 on both post- and pre-breeding migration compared to 2008 (Table 1). Overall, mean departure and arrival dates varied by 4 to 17 days between years on post-breeding migration, whereas pre-breeding migration was more synchronised with mean departure and arrival dates differing by just 1 to 5 days.

Duration of migration and stopover behaviour

Chatham Albatrosses showed substantial variation in the duration of migration, taking between 7 and 36 days to cross the South Pacific. This variation was observed in each year of the study period (2008-2010). Out of the 45 individuals tracked in this study, 36 (80 %) stopped while on migration for periods of 3 to 26 days. Birds stopped no more than two times during each post- or pre-breeding migration, yet more than two thirds (26 out of 36) stopped just once on either post- or pre-breeding migration. The overall percentage of birds stopping over was similar each year (75 % in 2008, 81 % in 2009 and 65 % in 2010). In 2008 equal numbers of birds (9) stopped during each post- and pre-breeding migrations, while in 2009 and 2010 more than twice as many birds made stopovers on pre-breeding migration (21 and 17 birds, respectively) compared to post-breeding migration (13 and 7 birds, respectively; Table 2). As observed for the total duration of migration, the range of stopover durations remained similar between years with a minimum duration of three days in all years and a maximum duration of 26, 22 and 20 days, respectively, in 2008, 2009 and 2010. The migration duration for birds commuting without stopovers varied between 7 and 22 days, whereas individuals who stopped took between 11 and 36 days.

Variation in the duration of migration was best explained by a combination of three factors: year, migration direction, and stopover duration. Model comparison based on the Akaike Information Criterion showed that out of 27 *a priori* candidate models, testing for the

effects of four different explanatory variables (see Methods), only one model (including all three of the named factors interacting with one another) received substantial support (Δi <2; Table 3). The probability for this model to fit the data best was 65 % ($Wi = 0.65$; Table 3) compared to 13 % for the second best model (evidence ratio = 5.04). The combination of explanatory factors was superior to the effect each factor would have on the duration of migration independently. Furthermore, all top ranking models (top five shown in Table 3) included stopover duration and thus outperformed models that included stopover event (yes/no), indicating that the latter factor did not suffice to explain the observed variance in duration of migration. The combinations and interactions of the explanatory factors within the top model set also suggest that the link between year and stopover duration is less strong than between each of those factors and migration direction. According to the best model (Table 3), the effect of migration direction (= differing lengths of migration on post- and pre-breeding migrations) depended on the year in which the migration took place, and the effect of stopover duration (= duration of migration increases as a function of stopover duration) again depended on the interaction of year and migration direction. While it made no difference whether the birds were on post- or pre-breeding migration in 2008, in both 2009 and 2010 the duration of pre-breeding migration was on average a week longer (7 and 8 days, respectively) than post-breeding migration (see 'total' in Table 2). Furthermore, in 2009 and 2010 the mean duration of post-breeding migration was 5-6 days shorter than in 2008, while on pre-breeding migration birds on average took 3-4 days longer in 2009 and 2010 to return to their breeding grounds compared to 2008 (Table 2). The mean total migration duration of birds stopping over was generally longer on both post- and pre-breeding (7-9 and 10-11 days, respectively, in 2008-2010; Table 2 and Figure 3). Yet the differences in the duration of post- and pre-breeding migration in 2009 and 2010 became apparent no matter if birds made stopovers or not (Figure 3), thus this difference could not be explained by the fact that more individuals stopped on pre-breeding than on post-breeding migration in 2009 and 2010 (Table 2). The duration of stopovers however was also influenced by the interaction of year and migration direction as described above.

Similar to observations for general migration, the mean duration of stopovers was 5-6 days longer on pre-breeding than on post-breeding migration in 2009 and 2010, while in 2008 no clear difference became evident (Table 4). Moreover, stopovers on post-breeding migration were on average 5 days shorter in 2009 and 2010 than in 2008. Unlike findings for total migration, the mean stopover duration on pre-breeding migration did differ less than a

day between years. However, due to a considerable degree of variation in the duration of migration in birds which did not stop over, resulting in some birds taking longer on migration without stopovers compared to those including stops, the increase of migration duration as a function of stopover duration became only apparent once stopovers lasted for more than 7 days (in 2010) or more than 10 days (in 2008 and 2009; Figure 4).

Spatial and temporal patterns of stopover sites

No obvious spatial patterns (e.g. clustering) could be identified for stopover sites along the migration pathway of Chatham Albatrosses. Stopovers occurred over the entire general migratory range of the birds (95% kernel) on both post-and pre-breeding migrations (Figure 5). Likewise, longer or shorter stopovers did not seem to follow any concise spatial pattern nor did they appear in distinct clusters. However, there was a slight notion of accumulations of stopover sites being split into a western and eastern half of the migration pathway.

Activity patterns

Comparisons of 29 *a priori* candidate models testing for effects of four different explanatory variables ('time of day', 'migration status', 'migration direction' and 'year') on the proportion of time spent on the water (activity state = 'wet') or alternating between landing and take-off (activity state = 'mix'), resulted in 'global' models (= all variables included) having the most explanatory power regarding the activity patterns detected (Table 5). In both cases, the model including interactions between all four explanatory variables was ranked highest, comprising almost 100 % of the probability of being the best model to fit the observed data distribution. Although categorised as 'very unlikely' according to their Δi values (Mazerolle 2004), subsequent models closest to the top model were considered in terms of interpreting the strength of interactions between factors, and also to account for the possibility that the top model was slightly overrated due to high complexity (e.g. recommended by Burnham et al. 2011).

The fact that all explanatory variables did enter into the best fitting models indicates that the effect of these variables on the observed characteristics in activity patterns of Chatham Albatrosses is biologically meaningful. However, in case of time spent on the water (activity state 'wet'), the combination of interactions between variables expressed in the top ranking models suggest the link between time of day ('daynight') and migration status ('status') was less important than the interaction of each of those two parameters with migration direction ('direction') and year ('yr'; Table 5). Moreover, the effect of time of day as well as migration

status appears to be almost strong enough to explain the variance in the proportions of time spent on water independently (i.e., without interaction) from the other explanatory variables. As for the time spent alternating between landings and take-offs (activity state 'mix'), the combinations within top ranking models suggested the link between time of day and migration status was more influential than the interaction with either migration direction or year (Table 5).

Activity state 'wet'

Chatham Albatrosses on migration generally spent less time on the water (activity state 'wet') during the day than at night (Figure 6). This pattern persisted in all three years of the study (2008-2010), during post- and pre-breeding, and during both continuous migration and stopover legs, with the average night time activity being 19.7% up to 39.8% higher than daytime activity (Table 6). However, the mean percentage of time spent on the water on while on a stopover always higher than on continuous migration, during both day and night (Table 6 and Figure 6a), indicating an increase in residency time. Furthermore, mean percentages of time spent on the water were lower on pre-breeding than on post-breeding migration (Table 6)

Activity state 'mix'

Mean proportions of time spent alternating between landing and take-off (activity state 'mix') were higher during the day than during night (Table 6 and Figure 6). However, the difference in 'mix' activity between day and night became mainly apparent during stopovers. Here, the mean proportion of time spent in respective activity state ranged from being 7.4% and up to 15.8% higher during day than at night, while during legs of continuous migration these differences showed up less strongly, ranging from 0.6% to 5.9% (Table 6). Moreover, the mean percentages of 'mix' activity on stopovers during the day were considerably higher than on continuous migration, while no obvious differences were detected at night (Figure 6b). These general patterns persisted across years regardless the direction of migration. However, the mean proportions of 'mix' behaviour were lower on pre-breeding compared to post-breeding migration (Table 6).

Table 1: Mean departure and arrival dates and the temporal range of post- and pre-breeding migration of Chatham Albatross during 2008-2010.

Species	Direction	Event	Year	N	Mean	SE	Minimum	Maximum
Chatham Albatross	post-breeding	departure	2008	16	03-Mar-2008	4 d	29-Jan-2008	03-Apr-2008
			2009	32	19-Feb-2009	3 d	21-Jan-2009	30-Mar-2009
			2010	29	24-Feb-2010	3 d	26-Jan-2010	06-Apr-2010
		arrival	2008	16	21-Mar-2008	4 d	25-Feb-2008	09-May-2008
			2009	32	04-Mar-2009	3 d	05-Feb-2009	18-Apr-2009
			2010	29	08-Mar-2010	3 d	10-Feb-2010	18-Apr-2010
	pre-breeding	departure	2008	16	23-Jun-2008	4 d	14-May-2008	26-Jul-2008
			2009	31	24-Jun-2009	3 d	28-May-2009	05-Aug-2009
			2010	27	19-Jun-2010	3 d	18-May-2010	24-Jul-2010
		arrival	2008	16	10-Jul-2008	5 d	21-May-2008	09-Aug-2008
			2009	31	15-Jul-2009	2 d	18-Jun-2009	19-Aug-2009
			2010	27	10-Jul-2010	3 d	15-Jun-2010	07-Aug-2010

Table 2: Mean migration duration of Chatham Albatross in three consecutive years (2008 – 2010) during post- and pre-breeding migration. The data is grouped into "total" (= including migration durations for all birds, with or without stopovers), "incl. stopover" (= migration durations of birds whose migration included stopovers) and "no stopover" (= migration durations of birds who migrated without stopovers). Presented are the number of individuals tracked (n) and the mean duration of migration (days ±SE) per group.

Year	Post-breeding migration						Pre-breeding migration					
	total		incl. stopover		no stopover		total		incl. stopover		no stopover	
	n	mean	n	mean	n	mean	n	mean	n	mean	n	mean
2008	16	18.7 (±2.0)	9	22.8 (±2.6)	7	13.4 (±1.7)	16	17.7(±1.6)	9	22.0 (±2.6)	7	12.1 (±1.1)
2009	32	13.9 (±0.8)	13	18.5 (±0.8)	19	10.7 (±0. 7)	31	21.2 (±1.2)	21	24.5 (±1.2)	10	14.2 (±0.7)
2010	29	12.4 (±0.8)	7	17.1 (±1.8)	22	10.9 (±0.6)	27	20.5 (±1.4)	17	24.9 (±1.4)	10	13.0 (±0.5)

Table 3: Results of the top five linear mixed effects models (fitted by maximum likelihood) used to explain the duration of migration of Chatham Albatross in 2008-2010. Models were selected based on the Aikaike Information Criterion out of a set of 25 *a priori* candidate models, including 'ID' as a random effect and different combinations of explanatory factors as fixed effects. Presented are models which comprise 98% of the probability (Cum. W*i*) of being the best model within the candidate set. All models shown have a Δi of <10 above which models are considered to be unlikely to fit the data reliably (Mazerolle 2004).

Model terms: mdur = migration duration [days]; yr = 2008, 2009, 2010; direction = post- and pre-breeding migration; sdur = stopover duration [days].

Model	K[a]	AICc	Δi [b]	W*i* [c]	Cum.W*i*	LL[d]
mdur ~ yr * direction * sdur	14	-20.66	0.00	0.65	0.65	25.87
mdur ~ yr * direction + sdur * direction	10	-17.42	3.23	0.13	0.78	19.50
mdur ~ direction * sdur	6	-17.39	3.27	0.13	0.90	14.98
mdur ~ yr * direction + sdur	9	-15.61	5.05	0.05	0.95	17.44
mdur ~ yr + direction * sdur	8	-14.33	6.32	0.03	0.98	15.67

[a] Number of parameters and interaction levels addressed in the model, including the intercept and residual variance.

[b] Difference between model AICc and minimum AICc value.

[c] Probability of model *i* being the best in this set of candidate models.

[d] Log likelihood.

Table 4: Stopover duration observed in Chatham Albatross over three consecutive years (2008 – 2010) during post- and pre-breeding migration. Presented are the number of birds tracked (n) and the mean duration of stopovers (days ±SE).

Year	Post-breeding migration		Pre-breeding migration	
	n	mean	n	mean
2008	9	10.0 (± 2.5)	9	11.8 (± 2.1)
2009	13	5.7 (± 0.7)	21	10.9 (± 1.2)
2010	7	5.6 (± 0.9)	17	11.3 (± 1.2)

Table 5: Results of the top four linear mixed effects models (fitted by maximum likelihood) used to explain the proportion of time spent by Chatham Albatross at either sitting on the water (activity state 'wet') or alternating between landings and take offs (activity state 'mix') during migration in 2008-2010. Included are only birds which made stopovers to allow for comparisons between continuous migration and stopover. Models were selected based on the Aikaike Information Criterion out of a set of 27 *a priori* candidate models, including 'ID' as a random effect and different combinations of explanatory factors as fixed effects.

Model terms: act.wet / act. mix = proportion of activity state [%]; status = continuous migration and stopover; daynight = day (light period) and night (dark period); direction = post- and pre-breeding migration; year = 2008, 2009, 2010;

Model	K[a]	AICc	Δ*i* [b]	W*i* [c]	Cum.W*i*	LL[d]
act.wet ~ status*yr* direction *daynight	25	9303.27	0.00	1.00	1.00	-4624.23
act.wet ~ status*yr* direction + daynight*yr* direction	19	9447.08	143.80	0.00	1.00	-4703.16
act.wet ~ daynight* direction *yr + status	14	9727.99	424.71	0.00	1.00	-4849.24
act.wet ~ status*yr* direction + daynight	14	9805.05	501.78	0.00	1.00	-4887.78
act.mix ~ status*yr* direction *daynight	25	3362.30	0.00	1.00	1.00	-1653.74
act.mix ~ status*daynight* direction + yr	11	3469.15	106.85	0.00	1.00	-1723.11
act.mix ~ status * direction * daynight	9	3515.49	153.19	0.00	1.00	-1748.43
act.mix ~ status*daynight*yr + direction	14	3612.05	249.75	0.00	1.00	-1791.28

[a] Number of parameters and interaction levels addressed in the model, including the intercept and residual variance.

[b] Difference between model AICc and minimum AICc value.

[c] Probability of model *i* being the best in this set of candidate models.

[d] Log likelihood.

Table 6: Mean proportions of time spent in two different activity states 'wet' and 'mix' by Chatham Albatross on migration in three consecutive years (2008-2010). Data are grouped by 'migration direction' (post- and pre-breeding), 'migration status' (continuous migration and stopover), and light ('day') and dark ('night') periods. Presented are the number of birds tracked (n) and the mean percentages of 'activity events' (% ±SE).

Activity state	Year	Post-breeding migration								Pre-breeding migration							
		continuous migration				stopover				continuous migration				stopover			
		day		night		day		night		day		night		day		night	
		n	mean	n	mean	n	mean	n	mean	n	mean	n	mean	n	mean	n	mean
wet	2008	9	18.7(±3.5)	9	50.8(3.8±)	9	34.7(±4.6)	9	71.2(±3.3)	9	6.9(±1.8)	9	26.6(±3.4)	9	25.9(±2.9)	9	54.4(±3.4)
	2009	13	16.9(±1.7)	13	46.5(±4.3)	13	24.8(±1.9)	13	64.6(±5.1)	21	7.2(±1.2)	21	27.5(±2.4)	21	22.3(±2.2)	21	48.5(±3.1)
	2010	6	18.9(±5.1)	6	40.7(±5.9)	6	33.2(±6.2)	6	65.5(±8.5)	16	8.1(±1.3)	16	34.6(±2.2)	16	17.1(±2.1)	16	54.5(±4.4)
mix	2008	9	24.1(±2.2)	9	20.1(±2.7)	9	34.8(±3.5)	9	22.4(±2.9)	9	20.1(±0.9)	9	19.5(±1.3)	9	34.6(±2.1)	9	19.9(±1.8)
	2009	13	24.7(±1.6)	13	21.9(±2.1)	13	31.2(±2.4)	13	23.8(±3.6)	21	20.7(±1.3)	21	18.2(±0.7)	21	36.4(±1.8)	21	20.6(±1.3)
	2010	6	24.3(±1.9)	6	18.9(±0.9)	6	30.5(±2.1)	6	21.1(±3.2)	16	22.1(±0.8)	16	16.2(±0.7)	16	33.4(±2.4)	16	19.3(±1.8)

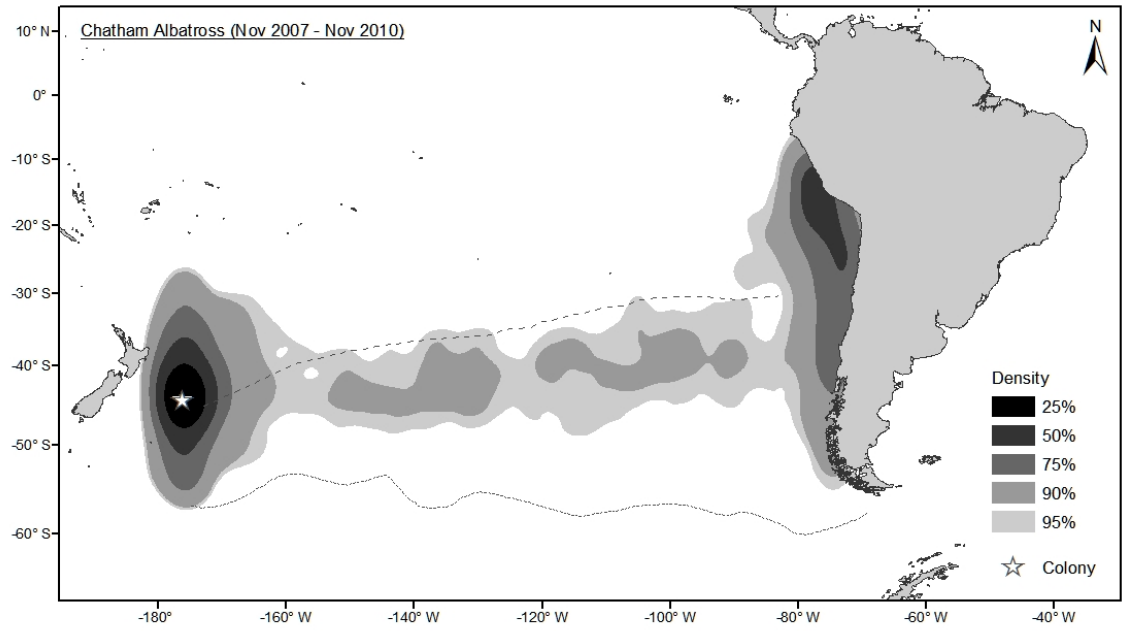

Figure 1: Kernel density estimates showing the distribution of 45 Chatham Albatrosses over the course of three years (2008-2010) within their breeding-, migration- and non-breeding ranges. The star shows the location of the breeding grounds in the Chatham Islands. Approximate locations of frontal systems as adopted from Orsi and Harris (2001, updated 2008) are shown as dashed (= Suptropical Front, STF) and dotted (= Subantarctic Front, SAF) lines.

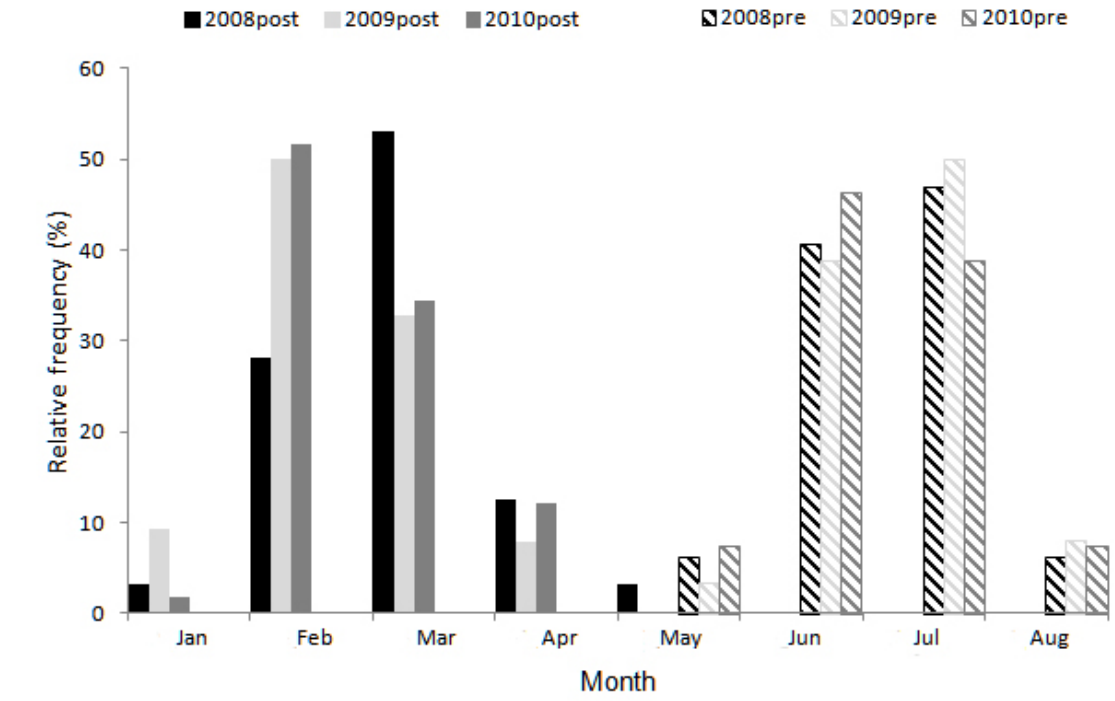

Figure 2: Relative frequencies of Chatham Albatrosses recorded on migration per month during 2008 to 2010. Filled bars show frequencies on post-breeding migration ('post'), hatched bars show frequencies on pre-breeding migration ('pre').

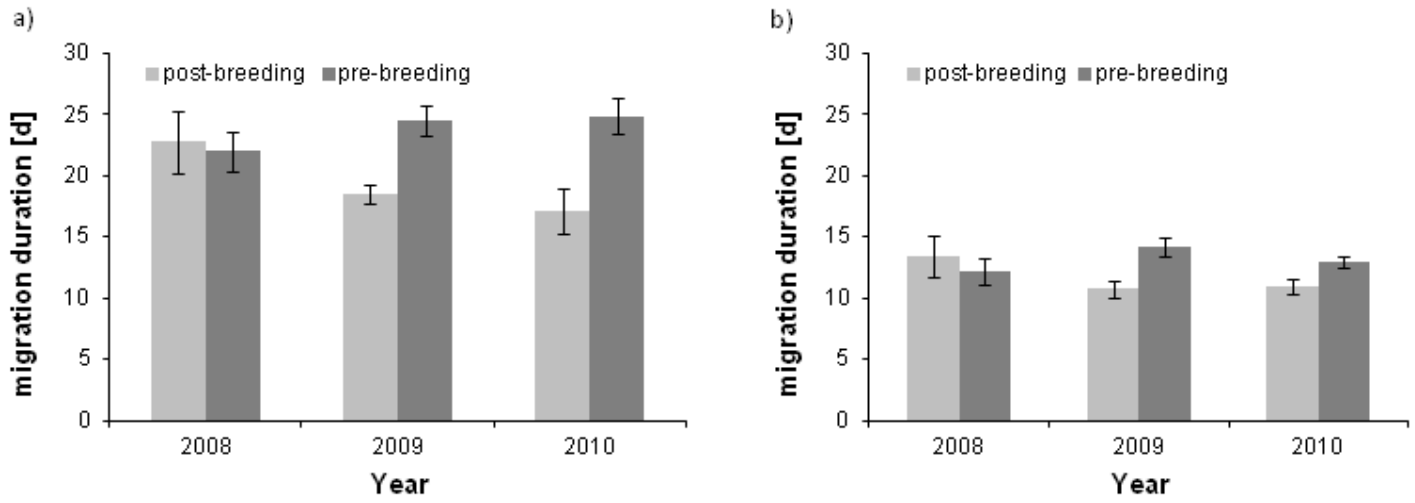

Figure 3: Mean migration duration (days ± SE) of Chatham Albatrosses on post- and pre-breeding migration over three consecutive years (2008-2010). a) shows migration including stopovers, b) shows migration without stopovers.

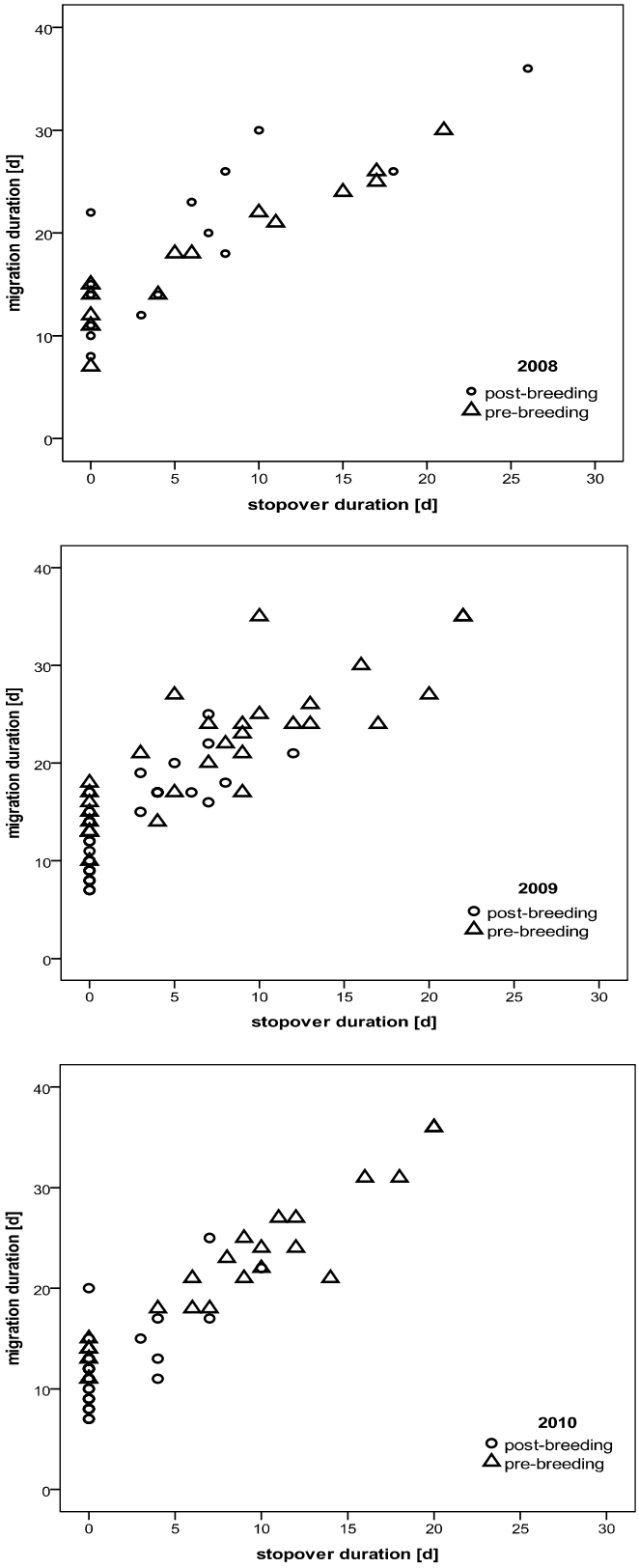

Figure 4: Migration duration as a function of stopover duration observed for Chatham Albatrosses tracked over three consecutive years (2008-2010).

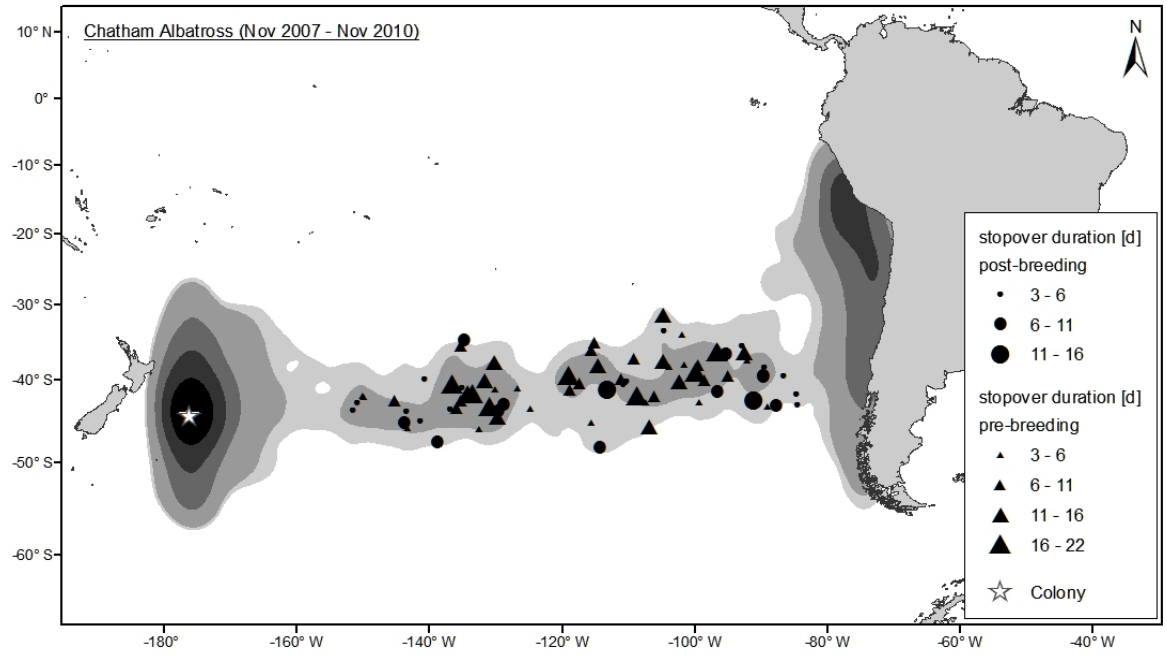

Figure 5: Stopover sites of Chatham Albatrosses tracked in 2008-2010 in relation to migration direction (post- and pre-breeding) and stopover duration (days), superimposed on kernel density estimates of the birds general distribution (see Figure 1 for legend on densities). The star shows the location of the breeding grounds in the Chatham Islands.

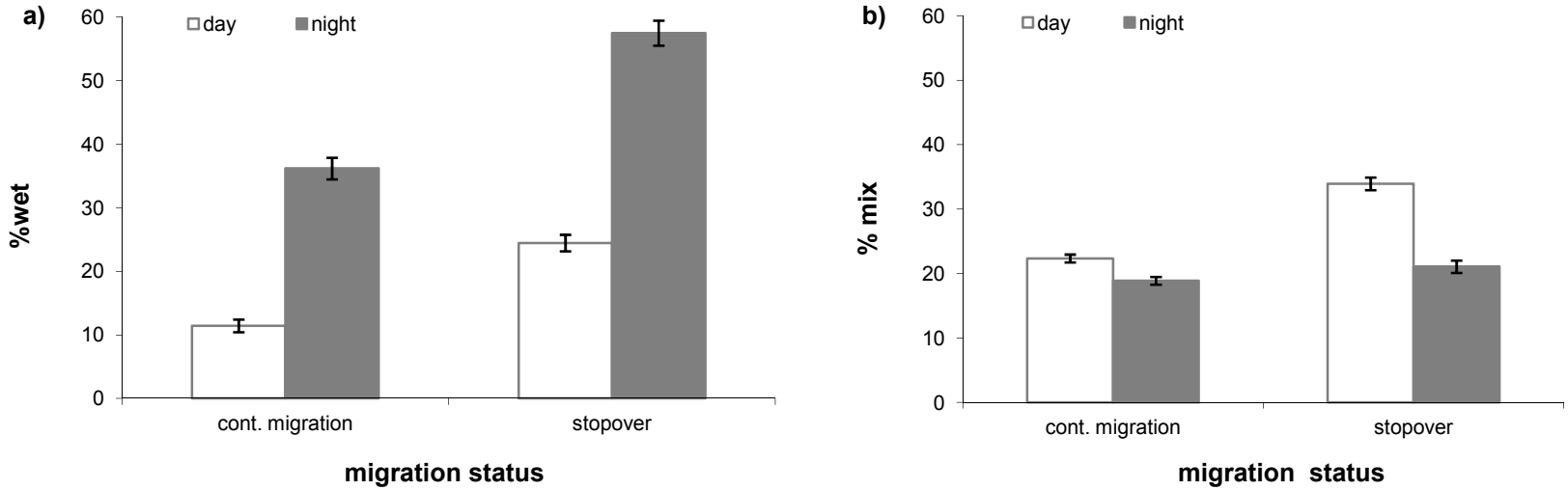

Figure 6: Mean proportions of time (% ±SE) spent in two different activity states a) 'wet' and b) 'mix' by Chatham Albatrosses during 'continuous migration' and 'stopovers'. Activity data is distinguished by light ('day') and dark ('night') periods.

DISCUSSION

The study of migratory patterns in Chatham Albatrosses, using GLS tracking devices with integrated immersion sensors, provided new insights into the migration strategies of the species. According to the terminology used by Dingle and Drake (2007), Chatham Albatrosses perform 'to-and-fro' migration, following the same route on post- and pre-breeding migrations between breeding and non-breeding grounds. This appeared to be a fixed pattern for the species, at least for adult breeders, since not a single deviation from this strategy was observed over the three years of this study. I also found that stopovers on migration are a common pattern in Chatham Albatrosses, although individuals did not seem to use traditional or shared stopover sites. The comparative analysis of behaviour during stopovers and continuous migration indicated enhanced foraging activity on stopovers. This, combined with comparatively little synchronicity in the timing of migration as well as considerable variation in the duration of migration itself, gives evidence that the majority of birds exploit their migration habitat opportunistically by following a 'fly- and forage' migration strategy (Klaassen et al. 2012), thus favouring the minimization of energy costs over the minimization of time on migration.

Migration route

Over the three years of the study, Chatham Albatrosses were found to move consistently along a mean latitude of 40°S when crossing the South Pacific between the Chatham Islands and South America on both post- and pre-breeding migrations. These findings are consistent with the course of Chatham Albatross tracks resulting from satellite tracking studies conducted in the 1990's and published in BirdLife International (2004), and with the observation of birds arriving "in a broad band along the South American coast between 30°S and 50°S" (Robertson and Nicholls in BirdLife International 2004). Other Procellariiformes breeding in New Zealand and wintering in South American waters, like Northern Buller's Albatross, *Thalassarche bulleri platei* (unpublished data), Southern Buller's Albatross, *Thalassarche bulleri bulleri* (Stahl and Sagar 2000), Northern Royal Albatross, *Diomedea epomophora sanfordi* (ACAP 2009b), Chatham Petrel, *Pterodroma axillaris* (Rayner et al. 2012) and Westland Petrel, *Procellaria westlandica* (Landers et al. 2011), have been found to migrate along similar latitudes as Chatham Albatrosses. Yearly consistencies as well as the use of a common migration route by different species at different times of the year due to species-specific migration schedules, emphasizes that the choice of the general course of this

route is not a major subject to seasonal changes. It also indicates that different species might exploit the same environmental conditions (e.g. wind patterns, forntal systems) on migration within the same geographical range.

Timing of migration

Chatham Albatrosses showed little synchronicity in the departure and arrival dates of both post- and pre-breeding migration. Synchronicity has been found to result from migration being scheduled according to lunar cycles (Pinet et al. 2011), the need for birds to pass through restricted flyways at a certain time (Shaffer et al. 2006) or avoiding usurpation of nest sites by prospecting congeners (Phillips et al. 2006). Yet, variable departure and arrival dates on migration have been observed in several other albatross and petrel species (Mackley et al. 2010; Landers et al. 2011; Rayner et al. 2012), but petrels appear to have a more synchronised migration schedule than that present in most albatrosses (Phillips et al. 2006; Mackley et al. 2011; Pinet et al. 2011). The variation within the migration dates of Chatham Albatrosses remained consistent over the three years of the study, and the same variability (at least during post-breeding migration) was observed in preliminary tracking studies of the species in the 1990's (BirdLife International 2004). This indicates not only a considerable degree of individuality generally inherent to Chatham Albatrosses, but also that the species does not rely on temporally strongly restricted environmental conditions or resources when it comes to migration.

The especially large variability observed in post-breeding departure dates of Chatham Albatrosses, ranging from late January to early April, may result from failed breeders leaving their breeding site earlier in the season. This behaviour seems to be common and has been observed in other Procellariiformes (Phillips et al. 2005; Mackley et al. 2010; Hedd et al. 2012). Unfortunately, the logistics of this study as well as the nature of the available GLS tracking data did not allow me to assess individual breeding success. According to the literature, chick fledging in Chatham Albatrosses occurs mainly during March and April (Robertson et al. 2003; ACAP 2009a), thus individuals migrating in January and February were probably failed breeders. However, it cannot be ruled out that some failed breeders may remain at the colony to defend their nest site against prospecting birds (as observed in Chatham Albatrosses during field work) and thus might not leave before successful breeders. When available breeding habitat is restricted, as it seems likely on The Pyramid (only 1.7 ha of breeding area), it may be advantageous for failed birds to remain at the breeding grounds

to secure their nest site. This could outweigh any potential benefit of reaching non-breeding grounds early. Similar circumstances might be the reason for Chatham Albatrosses consistently returning to their breeding site at least one or two months before their estimated egg laying dates in September/October (ACAP 2009a).

Duration of migration

The variation in the duration of migration of Chatham Albatrosses (7-36 days) remained consistent over the three study years and also corresponds to findings of Robertson and Nicholls (in BirdLife International 2004) who reported migration duration to differ between 11 and 30 days according to satellite tracking studies in the 1990's. Of the two petrel species recently tracked within the same migratory range as Chatham Albatrosses, Westland Petrels migrated considerably faster, taking just 4-13 days (Landers et al. 2011), whereas Chatham Petrels appeared to resemble Chatham Albatrosses with average migration durations of 20-23 days (Rayner et al. 2012; no range given). Thus, there is clear inter- as well as intra-specific variation in the time used to cover the same distance on migration but the reasons for these interspecific differences are not known and will require further study of a range of other species before general patterns can be discerned and their causes determined.

In Chatham Albatrosses in the current study, the duration of migration corresponded to the duration of stopovers made. Yet, this did not explain the variation found in the number of days the birds took to cross the South Pacific without stopovers (7-22 days). Moreover, seasonal patterns (i.e., differences observed in migration duration amongst years or for the direction of migration) appeared to affect migration with and without stopovers in the same way. As Robinson et al. (2009) stated, the precise timing of migration appears flexible and may be modified by conditions en route. Robertson and Nicholls (in BirdLife International 2004) considered becalming weather conditions as a possible explanation for prolonged migration as well as "areas of concentration" in the South Pacific. Similarly, Suryan et al. (2006) found evidence that non-breeding Short-tailed Albatrosses (*Phoebastria albatrus*) tend to aggregate in areas of low wind conditions.

Environmental factors influencing migratory patterns

Wind patterns

It is assumed that the common route of non-equatorial post-breeding migration in the South Pacific region is driven by strong prevailing westerly winds (Landers et al. 2011; Rayner et al. 2012). Stahl and Sagar (2000) observed two Southern Buller's Albatross individuals

using low pressure systems to progress rapidly downwind and slowing down when caught up in a high pressure ridge during post-breeding migration (eastward travel) across the South Pacific, resulting in alternating bouts of fast and slow travel. Several authors have described wind patterns such as strength and direction as influential on long-distance movements in seabirds (Felicísimo et al. 2008; Gonzalez-Solis et al. 2009; Adams and Flora 2010; Egevang et al. 2010; Pinet et al. 2011) and albatrosses are able to achieve very low flight costs when making use of favourable winds (Weimerskirch et al. 2000). Gonzalez-Solis et al. (2009) even observed in three different species of shearwaters that birds chose longer routes on migration in favour of minimizing flight costs by travelling along so-called "wind highways". Yet, the described migration corridor of Chatham Albatrosses across the South Pacific was used on both post- and pre-breeding migrations, thus birds were facing head winds when returning to their breeding grounds. Here, following the most direct route appears to outweigh the now less favourable effect of wind patterns. Guilford et al. (2009) similarly observed wind conditions being less important for the homeward migration of Manx Shearwater (*Puffinus puffinus*) in the Atlantic region.

Head winds were suggested by Landers et al. (2011) to cause slower pre-breeding (westwards) migration in Westland Petrels as well as more frequent breaks to rest and possibly forage when crossing the South Pacific. This would fit with the current findings for Chatham Albatrosses in 2009 and 2010, where likewise more birds made stopovers during pre-breeding migration, and mean migration as well as stopover durations were also longer. However, this was not the case in 2008 when post- and pre-breeding migration of Chatham Albatrosses neither differed in duration nor in the number of birds stopping over. Rayner et al. (2012) likewise found no differences between post- and pre-breeding durations of migration in Chatham Petrels on the same route in 2009. Guilford et al. (2009) observed that stopovers of Manx Shearwater coincided with strong head winds, but stated that this was not a universal pattern with some stopovers outlasting the duration of adverse weather conditions. All this may suggest that different species react differently to the same conditions, but it also may reflect reactions to conditions which vary on a finer scale at different times of the year or amongst years. Interestingly, none of the species moved faster on pre-breeding compared to post-breeding migration, which one may expect given the need to claim nest sites, pair up and breed in time, and what is found in other species of seabird (Egevang et al. 2010). This supports the assumption that prevailing wind conditions (favourable or unfavourable) may have a general impact on the progress of migration in species crossing the South Pacific.

Frontal systems

The migration route of Chatham Albatrosses lies within an area described as the subtropical front (STF), where subantarctic surface waters of the Antarctic Circumpolar Current meet the much warmer and saltier subtropical ocean regime, resulting in enhanced meridional gradients of sea surface temperature and salinity (Orsi and Whitworth 1995; Spalding et al. 2012). Oceanic fronts are known to provide favourable feeding conditions for apex predators like seabirds, however, prey aggregates patchily over space and time (Schneider 1990; Bost et al. 2009). Such patterns of food availability along the migration pathway of Chatham Albatrosses could be considered to induce the occurrence of stopovers, as birds may react to temporary foraging opportunities along the way in an opportunistic manner. This could also explain the spatially rather random distribution of stopover sites. The behaviour of combining migration with foraging in this manner is similar to what Suryan et al. (2006) observed in Short-tailed Albatrosses, although triggered by water column productivity along the North Pacific continental shelf and slope. Klaassen et al. (2012) observed so-called 'fly-and-forage migration' in gull species, suggesting the birds were following an energy selective rather than a time selective migration strategy.

Activity patterns on migration

Activity patterns during 'continuous migration' of Chatham Albatrosses showed that even active commute includes periods on the water, which are more pronounced during night than day. This complies with findings for other albatross species on migration (Mackley et al. 2010). The fact that Chatham Albatrosses could cross the South Pacific in as little as 7 days points out that it is not a necessity to stop en route to break up the journey. Yet, when on a stopover, Chatham Albatrosses spent more time sitting on the water during both day and night compared to periods of active commute. Similar results were found in shearwater species for which stopover behaviour was analysed in comparison to normal migration (Dias et al. 2011; Hedd et al. 2012). Apart from highlighting possible resting behaviour, such activity pattern can indicate intensified feeding, following the 'sit and wait' technique as observed in other albatross species (Prince and Francis 1984; Weimerskirch et al. 1997; Mackley et al. 2010). This foraging strategy is thought to be used more at night than during day due to visual limitations in targeting prey (Weimerskirch et al. 1997; Weimerskirch and Guionnet 2002), which is consistent with the finding that on stopovers Chatham Albatrosses spent larger proportions of time on the water at night than during day.

Increased landing and take-off behaviour during daylight compared to night time has been described as a second and more active foraging strategy (Weimerskirch et al. 1997; Weimerskirch and Guionnet 2002), and was observed in Chatham Albatrosses only on stopovers but not during legs of continuous migration. Higher landing rates during the day stopovers suggest that birds were actively foraging, and not just resting or waiting for a favourable wind (Dias et al. 2011). Birds could be moving between adjacent feeding spots, interacting with other birds feeding at the same spot, interacting with a fishing boat, or reacting to local prey enhancement by subsurface predators as observed by Yamamoto et al. (2010) for Streaked Shearwaters (*Calonectris leucomelas*) and Catry et al. (2009) for Wedge-tailed Shearwaters (*Puffinus pacificus*). This foraging strategy has so far mainly been reported in relation with feeding and foraging during periods of residence while breeding or wintering. Mackley et al. (2010) observed wintering Black-browed and Grey-headed Albatrosses (*Thalassarche melanophrys* and *T. chrysostoma*) engage in short flight bouts during daylight and concluded this was indicative of area-restricted searching within patches of high prey density, in which prey capture may require active pursuit by plunging and diving within competitive feeding flocks. Guilford et al. (2009) also reports that in Manx Shearwaters activity patterns on stopovers were more typical of summer and winter feeding than of active migration. Thus, the hypothesis that stopovers indeed are refuelling stops integral to seabird migration (Guilford et al. 2009) seems reasonable and has critical implications in terms of identifying important areas at sea within or along migratory pathways.

In the current study, the majority of Chatham Albatrosses were found to engage in stopovers, thus using the South Pacific offshore waters as a potential foraging habitat. General activity patterns remained consistent over the years of the study, confirming that behavioural differences between periods of continuous migration and stopovers were not random. Although no spatial clusters could be detected in the timing or distribution of stopover sites, key periods of migratory activity were identified, with March/April on post-breeding and June/July on pre-breeding migration being periods in the species' life cycle where individuals rely particularly on the environmental conditions of the offshore habitats traversed on migration. Respective areas have to be taken into account in conservation planning, for example by minimising potential conflict with fisheries and thus ensuring a safe and sustainable environment to be exploited by Chatham Albatrosses on migration.

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APPENDIX

Appendix 1: Departure and arrival dates during post- and pre-breeding migration of Chatham Albatross (= 'CA') tracked in 2008, 2009 and 2010. The duration of each migration period (per bird) is given in days [d].

			Post-breeding migration			Pre-breeding migration		
Year	**Species**	**ID**	**Departure**	**Arrival**	**Duration [d]**	**Departure**	**Arrival**	**Duration [d]**
2008	CA	33766	5/02/2008	25/02/2008	20	5/06/2008	27/06/2008	22
2008	CA	33743	9/03/2008	4/04/2008	26	27/06/2008	12/07/2008	15
2008	CA	33736	24/03/2008	16/04/2008	23	8/07/2008	1/08/2008	24
2008	CA	33775	28/02/2008	13/03/2008	14	25/06/2008	6/07/2008	11
2008	CA	33765	8/03/2008	18/03/2008	10	29/06/2008	17/07/2008	18
2008	CA	33742	29/01/2008	28/02/2008	30	14/05/2008	21/05/2008	7
2008	CA	33744	25/03/2008	6/04/2008	12	5/07/2008	31/07/2008	26
2008	CA	33741	7/03/2008	18/03/2008	11	28/06/2008	10/07/2008	12
2008	CA	33763	10/02/2008	25/02/2008	15	20/06/2008	5/07/2008	15
2008	CA	33737	29/02/2008	26/03/2008	26	8/06/2008	19/06/2008	11
2008	CA	33768	11/03/2008	25/03/2008	14	10/07/2008	28/07/2008	18
2008	CA	33754	17/03/2008	25/03/2008	8	5/07/2008	26/07/2008	21
2008	CA	33767	3/04/2008	9/05/2008	36	26/07/2008	9/08/2008	14
2008	CA	33745	4/03/2008	26/03/2008	22	7/06/2008	21/06/2008	14
2008	CA	33746	5/03/2008	19/03/2008	14	11/06/2008	6/07/2008	25
2008	CA	33764	9/02/2008	27/02/2008	18	22/06/2008	22/07/2008	30
2009	CA	33739	21/02/2009	10/03/2009	17	23/06/2009	17/07/2009	24
2009	CA	33764	21/02/2009	10/03/2009	17	22/06/2009	14/07/2009	22
2009	CA	33838	16/02/2009	8/03/2009	20	1/07/2009	18/07/2009	17

			Post-breeding migration			Pre-breeding migration		
Year	**Species**	**ID**	**Departure**	**Arrival**	**Duration [d]**	**Departure**	**Arrival**	**Duration [d]**
2009	CA	33767	15/02/2009	5/03/2009	18	3/07/2009	21/07/2009	18
2009	CA	33828	28/03/2009	18/04/2009	21	20/07/2009	15/08/2009	26
2009	CA	33763	10/03/2009	18/03/2009	8	5/07/2009	21/07/2009	16
2009	CA	33811	6/02/2009	15/02/2009	9	9/06/2009	22/06/2009	13
2009	CA	33863	15/02/2009	2/03/2009	15	29/06/2009	19/07/2009	20
2009	CA	33812	30/01/2009	6/02/2009	7	9/06/2009	9/07/2009	30
2009	CA	33745	5/02/2009	13/02/2009	8	4/06/2009	29/06/2009	25
2009	CA	33746	6/02/2009	23/02/2009	17	3/06/2009	30/06/2009	27
2009	CA	25556	28/03/2009	14/04/2009	17	17/07/2009	30/07/2009	13
2009	CA	33744	15/02/2009	9/03/2009	22	9/06/2009	26/06/2009	17
2009	CA	33821	9/03/2009	24/03/2009	15	4/07/2009	31/07/2009	27
2009	CA	33837	13/02/2009	27/02/2009	14	1/06/2009	6/07/2009	35
2009	CA	33737	31/01/2009	8/02/2009	8	28/05/2009	2/07/2009	35
2009	CA	33743	29/01/2009	8/02/2009	10	8/06/2009	18/06/2009	10
2009	CA	33741	21/01/2009	9/02/2009	19	10/06/2009	25/06/2009	15
2009	CA	33736	31/01/2009	17/02/2009	17			
2009	CA	33784	13/02/2009	25/02/2009	12	3/07/2009	7/08/2009	35
2009	CA	33742	8/02/2009	24/02/2009	16	29/05/2009	22/06/2009	24
2009	CA	33754	30/01/2009	6/02/2009	7	23/06/2009	14/07/2009	21
2009	CA	33765	27/01/2009	5/02/2009	9	5/08/2009	19/08/2009	14
2009	CA	33740	15/02/2009	1/03/2009	14	27/06/2009	21/07/2009	24
2009	CA	33833	9/03/2009	21/03/2009	12	2/07/2009	15/07/2009	13
2009	CA	33832	27/02/2009	9/03/2009	10	3/07/2009	26/07/2009	23
2009	CA	25144	9/03/2009	3/04/2009	25	29/06/2009	23/07/2009	24

			Post-breeding migration			Pre-breeding migration		
Year	**Species**	**ID**	**Departure**	**Arrival**	**Duration [d]**	**Departure**	**Arrival**	**Duration [d]**
2009	CA	33831	30/03/2009	9/04/2009	10	22/07/2009	15/08/2009	24
2009	CA	33822	18/02/2009	1/03/2009	11	22/06/2009	5/07/2009	13
2009	CA	33864	21/03/2009	4/04/2009	14	7/07/2009	28/07/2009	21
2009	CA	33766	13/02/2009	2/03/2009	17	22/06/2009	9/07/2009	17
2009	CA	33750	3/03/2009	12/03/2009	9	30/06/2009	14/07/2009	14
2010	CA	33900	3/02/2010	18/02/2010	15	18/05/2010	23/06/2010	36
2010	CA	33811	17/03/2010	26/03/2010	9	25/06/2010	6/07/2010	11
2010	CA	33919	11/03/2010	24/03/2010	13	17/07/2010	7/08/2010	21
2010	CA	33767	13/02/2010	23/02/2010	10			
2010	CA	33864	15/02/2010	28/02/2010	13	16/06/2010	9/07/2010	23
2010	CA	33741	18/02/2010	2/03/2010	12			
2010	CA	33746	2/02/2010	11/02/2010	9	24/05/2010	20/06/2010	27
2010	CA	33745	3/02/2010	25/02/2010	22	19/05/2010	19/06/2010	31
2010	CA	42147	8/02/2010	19/02/2010	11	3/06/2010	27/06/2010	24
2010	CA	33853	1/04/2010	18/04/2010	17	14/07/2010	28/07/2010	14
2010	CA	33739	24/02/2010	7/03/2010	11	20/06/2010	8/07/2010	18
2010	CA	33877	14/02/2010	25/02/2010	11	25/06/2010	8/07/2010	13
2010	CA	33921	13/03/2010	21/03/2010	8	20/06/2010	14/07/2010	24
2010	CA	33837	3/03/2010	14/03/2010	11	14/06/2010	28/06/2010	14
2010	CA	33859	26/01/2010	20/02/2010	25	13/06/2010	10/07/2010	27
2010	CA	33838	11/03/2010	24/03/2010	13	21/06/2010	9/07/2010	18
2010	CA	33922	26/02/2010	10/03/2010	12	1/06/2010	7/07/2010	36
2010	CA	33894	17/02/2010	9/03/2010	20	6/06/2010	27/06/2010	21
2010	CA	33750	1/04/2010	18/04/2010	17	14/07/2010	27/07/2010	13

			Post-breeding migration			Pre-breeding migration		
Year	**Species**	**ID**	**Departure**	**Arrival**	**Duration [d]**	**Departure**	**Arrival**	**Duration [d]**
2010	CA	33740	6/04/2010	13/04/2010	7	15/07/2010	2/08/2010	18
2010	CA	33754	3/02/2010	10/02/2010	7	17/06/2010	28/06/2010	11
2010	CA	33821	1/03/2010	13/03/2010	12	16/07/2010	27/07/2010	11
2010	CA	33833	3/02/2010	13/02/2010	10	7/06/2010	21/06/2010	14
2010	CA	33898	12/03/2010	25/03/2010	13	24/07/2010	7/08/2010	14
2010	CA	33828	10/02/2010	18/02/2010	8	26/06/2010	18/07/2010	22
2010	CA	25144	31/03/2010	8/04/2010	8	7/07/2010	7/08/2010	31
2010	CA	33872	10/02/2010	25/02/2010	15	24/06/2010	9/07/2010	15
2010	CA	33863	19/02/2010	3/03/2010	12	12/06/2010	7/07/2010	25
2010	CA	33737	5/02/2010	14/02/2010	9	25/05/2010	15/06/2010	21

CHAPTER 4

At-sea distribution and habitat selection of Chatham Albatrosses (*Thalassarche eremita*) during early chick rearing

ABSTRACT

Albatrosses respond to spatial heterogeneity in food abundance in relation to oceanic features. During breeding birds are subject to central-place constraints, which may make their success at foraging highly dependent on local environmental conditions and the spatial heterogeneity of food close to the colony. Using high resolution GPS tracking data, I studied the foraging distribution and habitat use of Chatham Albatrosses (*Thalassarche eremita*) breeding on The Pyramid in the Chatham Islands over three consecutive years (2007-2009) during early chick rearing. The extent of the foraging range for the species remained similar across the three years of the study, with 95% of the birds not venturing beyond the shelf-break area of the Chatham Rise. However, core areas tended to vary between years. Foraging trips lasted between 1 and 6 days, but birds making longer trips did not necessarily range further from the colony than on shorter trips. An analysis of associations between bird locations in 'high use' areas (i.e., potential foraging spots) and four different habitat parameters (bathymetry, slope, sea surface temperature [SST] and chlorophyll a concentration [Chl *a*]) showed that foraging events were not distributed randomly. 'High use' areas occurred most frequently in waters of <500 m depth, indicating a preference for foraging above the shelf. Birds also foraged at comparatively steeper slopes than expected from a random distribution, suggesting they actively included areas of shelf edges when searching for food. SST frequented by foraging birds varied between 14°C and 16°C in all years, which suggests consistent patterns in prey resources linked to this temperature range. Chl *a* concentrations found in association with potential foraging spots were relatively low in all years (< 2 mg/m^{-3}), although higher during the 2007 season, which may be related to La Niña related processes affecting the area. The results suggest that Chatham Albatrosses rely on resources that are overall predictable in location but they also respond to fine scale changes within their general foraging environment. Incorporating such fine scale dynamics in habitat use may prove challenging in conservation planning.

Keywords: Chatham Albatross, foraging behaviour, habitat use, environmental parameter

INTRODUCTION

In the quest to find food, both temporal and spatial scales are thought to influence the interaction of an animal with its foraging environment (Brown 2000). How efficiently an animal forages depends on its ability to source prey within the range of accessible habitats (Ceia et al. 2012). Wide-ranging seabirds like albatrosses can cover large distances in order to exploit their environment within which prey distribution is patchy and often unpredictable (Weimerskirch et al. 2005; Humphries et al. 2012). However, during the breeding season, albatrosses become central place foragers (Pinaud and Weimerskirch 2005) and are then subject to spatial as well as temporal limitations. Increased energy demands caused by incubation and chick rearing require a strategy that maximizes energetic gain, leading to increased dependence on available resources within foraging habitats closer to the colony (Young 2009). Under a conservation perspective it is therefore necessary to observe and understand patterns in foraging distribution and behaviour, in order to assess and mitigate threats to albatrosses during periods when they are particularly vulnerable. The protection of foraging areas during breeding is widely recognised as being important to breeding success in seabirds (Thaxter et al. 2012).

Albatrosses are versatile in their foraging strategies during breeding, and this can differ due to species-specific differences in breeding biology, stage of the breeding cycle, location of the breeding site, foraging behaviour, or type of prey targeted (Hedd et al. 2001; Huin 2002; Young 2009). Variation in these factors mainly affect features like the size of foraging ranges, trip duration, and location of foraging spots (Xavier et al. 2004; Phalan et al. 2007, Thaxter et al. 2012). Wandering Albatrosses (*Diomedea exulans*) for example can range as far as 15,000 km on a single foraging trip (Weimerskirch et al. 2007; Ceia et al. 2012), while others such as the Waved Albatross (*Phoebastria irrorata*; Awkerman et al. 2005), venture not much further than a hundred kilometres off their breeding colony. As observed in Light-mantled Sooty Albatrosses (*Phoebetria palpebrata*), which were forced to forage further away from their colony due to the presence of larger or more manoeuvrable species (Phillips et al. 2005), the extent of the foraging range can be altered by inter-specific competition. Nevertheless, the factor that probably has the greatest effect on foraging ranges in most albatross species is breeding stage, i.e., whether birds are engaged in breeding and thus tied to a nest or in the post-brood phase when this constraint is lifted (Phalan et al. 2007).

Contraction of foraging range, and shorter foraging trips during brood guard or early chick rearing, appears to be a common pattern in seabirds and has been linked with increased

time efficiency as well as increased energy demands when feeding chicks (Brothers et al. 1998; Huin 2002; Awkerman et al. 2005). There is however a certain amount of species-specific as well as individual variation within this pattern. Studies on Southern Buller's Albatross (*Thalassarche b. bulleri*; Stahl and Sagar 2000) as well as Black-footed (*Phoebastria nigripes*), Laysan (*P. immutabilis*) and Waved Albatross (Fernández et al. 2001) found that birds alternated between short and long foraging trips during chick rearing. The longer trips could be associated with birds exploiting habitats that were more predictable in terms of prey availability (Fernández et al. 2001), a benefit which may at least partly outweigh the advantage of searching for food closer to the colony. These short and long trips appear to correspond to two foraging strategies in albatrosses, where individuals either commute between their colony and a predictable or known foraging spot, or they are constantly searching while flying (usually in a loop pattern) and encountering prey at irregular intervals (Brothers et al. 1998; Catry et al. 2004). Birds may apply the different strategies according to different stages in the breeding cycle, depending on the prey targeted and/or the environmental conditions within their breeding habitat (Weimerskirch et al. 1993; Catry et al. 2004; Ceia et al. 2012). Within the marine environment they also have to respond to spatial heterogeneity in food abundance, according to different characteristics in oceanic features (Awkerman et al. 2005). Thus, habitat selection is further shaped by patch use, which again may or may not be exploited depending on diet choice (Brown 2000).

Both the distribution of albatrosses and their foraging behaviour have been linked to oceanic features, like shelf upwellings, seamount eddies and frontal zones, as well as certain temperature regimes, where potential prey is likely to accumulate (Brothers et al. 1998; Catry et al. 2004; Awkerman et al. 2005). It is commonly considered that bathymetric relief, sea surface temperature (SST), sea surface height, primary productivity (Chl *a*) and gradients thereof, determine prey abundance and hence seabird distribution (Hedd et al. 2001; Awkerman et al. 2005; Freeman et al. 2010). Foraging site-fidelity, as observed in several species, is assumed to result from certain oceanic characteristics which cause predictably located aggregations of prey in both time and space (Cherel et al. 2000). Nevertheless, annual variation found in foraging behaviour and habitat choice of breeding albatrosses (Xavier et al. 2004), suggests birds also respond to less permanent or predictable conditions under which food may become available. In this respect it is of interest to investigate whether, and in what way, birds follow or adjust their distribution according to annual changes in environmental characteristics.

To address questions of habitat choice and consistency in foraging range during breeding, I used high resolution GPS data received from tracking Chatham Albatrosses (*Thalassarche eremita*) in three consecutive years during chick rearing, the period when birds were assumed to particularly rely on the local environment. The Chatham Albatross is endemic to New Zealand, with the entire population breeding on a single rock stack (The Pyramid) in the Chatham Islands, located in the far east of New Zealand's extended continental shelf, the Chatham Rise. The species breeds annually and eggs are laid September/October, with hatching occurring in November/December, and the chicks fledging in March/April (ACAP 2009). Preliminary satellite tracking studies of breeding Chatham Albatrosses reported that birds foraged close to their breeding site along continental slope features of the Chatham Rise (Robertson & Nicholls in BirdLife International 2004). The reproductive success of Chatham Albatrosses appears to rely mainly on the conditions on the Chatham Rise and adjacent areas but no detailed studies in terms of habitat use have been undertaken to date. Chatham Petrels (*Pterodroma axillaris*), breeding at a neighbouring island, have been observed to venture far beyond the shelf and shelf break areas of the Chatham Rise during chick rearing, frequenting deeper waters as well as more distant foraging destinations like seamounts (Rayner et al. 2012). Featuring steep shelf slopes within the transition zone of the Subtropical and Subantarctic Frontal Systems, the Chatham Rise is a highly productive area and draws in a variety of other seabird species, but also a high level of commercial fishing activities (Nicholls et al. 2002). Increased mortality due to overlap with fisheries areas has been described for several albatross species, including those birds foraging in shelf areas (Fernández et al. 2001; Huin 2002; Waugh et al. 2005), and posing a potential threat for Chatham Albatrosses in the vicinity of their breeding island. Fisheries are a potential threat to breeding Chatham Albatrosses, by competing for the same resource and by killing birds during fishing operations (Robertson et al. 2003). Thus, an understanding of why birds forage in certain areas is needed to mitigate risk.

This study aimed to identify distributional patterns of Chatham Albatrosses at the population level and thus does not emphasize individual variability. Instead, the current study intends to contribute to the understanding of fine-scale distributional patterns of Chatham Albatrosses in general and the degree of annual variability within those patterns. For this purpose, I firstly describe the foraging extent and as well as trip duration during early chick rearing for Chatham Albatrosses over three consecutive years, and then investigate annual

differences in the associations of foraging birds with a selection of habitat parameters (bathymetry, slope, SST and Chl *a*).

METHODS

Logger deployment and recordings

The study was carried out at the breeding site of the Chatham Albatross on The Pyramid (44°25'S / 176°14'E) in the Chatham Islands, New Zealand, during early chick rearing (November/December) over three consecutive years (2007-2009). Foraging trips were recorded using miniaturized GPS data loggers (GiPSy, TechnoSmArt: 45 x 24 x 5 mm; 2.8 g; integrated Antenna) powered by rechargeable Lithium-Polymer batteries (1100 mAh; 2.45 V; 45 x 37 x 4 mm; 25.1 g). As a trade-off between high resolution recordings and maintaining battery power for a sufficient time, the data loggers were set to take 1 fix every 5 minutes and return to sleep mode if no successful fix could be achieved in a 3 minute period. Devices were attached with Tesa tape to the back feathers of adult breeders caught on the nest and were removed as soon as the bird was recorded to have returned. The overall weight of the logging device of 28 g corresponded to 0.8% of the average body mass of Chatham Albatrosses, thus it was below the recommended threshold of 3%, above which adverse behavioural effects could be expected (Phillips et al. 2003). All study birds were identifiable by carrying metal and sight bands.

In 2007, a total of 10 individuals were tracked between 19-26 November, delivering 12 complete foraging trips. Tracking of another 21 individuals from 11 November to 2 December 2008 resulted in 20 complete and 7 incomplete foraging trip recordings. Similarly, GPS devices placed on 18 individuals tracked from 24 November to 11 December 2009, provided data from 20 complete and 5 incomplete foraging trips. With 5 individuals being tracked during multiple years (four during 2007 and 2008, and one during 2007 and 2009), the total number of Chatham Albatrosses tracked over the three years of the study was 44 individuals.

Data analysis

Positional data downloaded from the GPS devices were processed in ArcGIS 9.3.1 (ESRI 2009) to derive the spatial and temporal extent, the course and the duration of the recorded foraging trips. Trip duration was measured in days, and only completed trips were included.

To visualize the general foraging distribution as well as overall core areas of Chatham Albatrosses during early chick rearing, kernel densities were calculated from the original tracking data using the Spatial Analyst extension in ArcGIS 9.3.1 (ESRI 2009) with a search radius of 40 km and an output cell size of 500 m. Resulting 25% and 50% kernel contours were used to describe core areas, while 95% kernel contours described the extent of the general area used by Chatham Albatrosses during foraging trips. Maps were plotted for each year to identify annual variation in the general spatial patterns. Additionally, annual core areas were superimposed onto each other in order to detect the occurrence of temporally and spatially consistent areas of general importance on visual inspection.

Locations recorded from birds being on land, and all locations within a 500 m wide range around the colony were removed prior to kernel analysis. It has been argued that high densities in the vicinity of breeding colonies would mainly result from locations of rafting or commuting birds and should be excluded from analysis in respect of foraging distributions, causing other authors to choose larger exclusion zones around breeding colonies (Awkerman et al. 2005; Torres et al. 2011). However, as the location of the breeding island of the Chatham Albatross coincides with the shelf break area of the Chatham Rise, and thus areas close to the colony may be potential foraging habitat, no additional locations were excluded from the analysis. This approach was supported by the detection of track patterns indicating possible foraging behaviour (i.e., accumulation of GPS points on a smaller scale as well as changes in path direction) in less than 1 km distance from the colony during visual inspection of the data.

The analysis of marine habitat parameters in relation to the foraging distribution of Chatham Albatrosses was focused to identify areas where birds were likely to have been engaged in actual foraging or feeding behaviour, i.e. where the birds slowed down or sat on the water, moved in small circles or at a constantly changing course, or patrolled an area by flying back and forth. Such areas could be identified via 25% as well as 50% contours from kernel density estimates on a fine scale (search radius of 5 km), based on the fact that these behaviours result in increased amounts of time spend in a defined area (defined here as ‘high use’ areas). The density clusters also likely included parts of the tracks where birds crossed a certain patch repeatedly while flying along a more or less straight line while commuting elswhere, especially when clusters were close to the colony. However, since those track patterns caused point accumulations at a smaller scale (5 km radius), and point accumulations along a straight path can also indicate interaction with fishing vessels or food intake during

commute (Catry et al. 2004; Torres et al. 2011), these clusters were included in subsequent analyses. Nevertheless, to account for the higher proportion of 'commuting' locations in the vicinity of the breeding colony, the smaller unit for describing 'high use' areas (25% kernel contour) was chosen to identify point clusters. For regions further away from the colony however, 50% kernel contours proved more appropriate to depict respective clusters. Bird locations within the identified 'high-use' or 'potential foraging' areas were used to sample the local environmental characteristics by spatially joining georeferenced point data with layers of environmental raster data in ArcGIS. Data sets of bathymetry and slope with a cell size of 1.2 km and 0.25 km, respectively, were provided by NIWA for the region of the Chatham Rise. Sea surface temperature (SST) and Chlorophyll a (Chl *a*) were derived from online servers (ftp: // podaac-ftp. jpl. nasa. gov / OceanTemperature / modis / L3 / aqua and http: // oceandata. sci. gsfc. nasa. gov / SeaWiFS / L3SMI). Monthly composites with a spatial resolution of 4 km and 9 km, respectively, were chosen to match the time frame within which foraging trips were recorded.

To test whether the distribution of environmental parameters frequented by Chatham Albatrosses within 'high use' areas was different from random, and thus infer whether the birds were utilizing specific environmental characteristics when engaging in foraging activity, random samples of habitat parameters were extracted from environmental raster data sets for comparison. Based on the number of actually recorded bird locations within 'high use' areas (1761 in 2007, 6368 in 2008 and 3280 in 2009), respective sets of random points were created within the general foraging range of the birds. The general foraging range was defined as a rectangular shape according to the N-S and E-W extent of the recorded foraging trips to account for the easterly skewed distribution of the birds. This range was selected to present the actual and not the potential foraging range used by the birds during chick rearing, and thus based on the actual measured extent during three years of chick rearing observed in this study. However, two foraging trips were excluded as 'outliers' in this procedure since they ranged beyond the area where most (> 95%) birds concentrated their foraging and would have lead to a considerable larger size of the sampling area which was not deemed reasonable for the purpose of this comparison. Two-sided Kolmogorov-Smirnov tests were used to identify significant differences between the frequency distributions of actual and randomly sampled values of bathymetry, slope, SST and Chl *a* during each year. Mean annual differences in the distribution of habitat characteristics within 'high use' areas were also addressed by fitting general linear mixed models (GLMM) to each of the environmental

parameter distributions, including year as fixed and bird ID as random effect. Standard linear models were fitted to evaluate the degree of individual variability each year, while potential consistencies in habitat associations of the same individuals across two years were tested using independent 2-group Mann-Whitney U Tests. Statistical tests were run in the R environment (R Development Core Team, 2010). Mean values are given ± SE.

RESULTS

General foraging distribution and high density areas

Foraging trips of Chatham Albatrosses during early chick rearing in November/December 2007-2009 were observed to range across the whole eastern half of the Chatham Rise, covering continental shelf as well as shelf break areas. The majority of birds (i.e., 42 out of 44) were recorded between 169.3 – 179.5 °W and 41.6 – 46.6 °S. The two exceptions were one individual that ranged as far east as 161.6 °W (region of Louisville Ridge) in 2009, while another one explored the Chatham Rise shelf further to west towards New Zealand's South Island, at 175.7 °E during the 2008 season. Chatham Albatrosses thus went as far as 1200 km from the colony, but most individuals did not extend their foraging trips further than 300 - 400 km away from the colony, and the odd bird stayed even within 30 km off the breeding island.

Although birds extended their trips further towards the east of the colony than towards the west in all three years of the study, the spatial extent of the foraging ranges varied among years (even with the 2 'outlier trips' excluded), being smallest in 2007 and largest in 2008 (Figure 1). The location of high density areas, i.e., areas which were used more intensely within the general foraging range in terms of time spent and which are described by the 25% and 50% kernel contours (Figure 1), were also subject to annual variation. Little spatial overlap was observed for high density areas of birds foraging on the continental shelf or along its northern shelf break (Figure 2). Only north-west of the main Chatham Island did core areas of birds in 2007 and 2009 overlap. In contrast, extensive overlap was found in the catchment of the breeding colony, which is also the southern shelf break area of the Chatham Rise. It has to be noted that in all three years these high density areas mainly extended towards the southeast of the colony, and thus were different from a circular shape which might be expected if birds commuted between potential foraging sites and colony in a random manner. Also noteworthy is the observation that the high density areas did not extend into

deeper waters but remained on the shelf or along the shelf breaks. The southern shelf break areas in particular (south and east of the colony) were intensely used by birds during the 2008 and 2009 seasons (Figures 1 and 2).

Trip duration

Generally, foraging trips of Chatham Albatrosses during early chick rearing lasted between 1 and 6 days with an overall mean duration of 2.8 ± 0.2 days (Table 1). The two individuals which ventured beyond the general foraging range were excluded from this analysis due to early termination of the trip recordings, and thus can be ruled out to have biased the range of trip duration in terms of maximum number of days. In 2007 birds only left the colony for 2 or 3 days, with a mean trip duration of 2.5 ± 0.1 days, which seemed to be in concordance with their comparatively more restricted general foraging range during the same year (Figure 1). Although the total range in trip duration was larger during the 2009 season (1-5 days), the average trip durations (2.3 ± 0.3 days) were even lower than in 2007, indicating that most birds were also doing shorter trips. In 2008, individuals tended to take longer foraging trips compared to the other two years, which lasted 3.5 ± 0.3 days on average.

Habitat parameter within 'high use' areas

As for the overall core areas, little spatial overlap of 'high use' (potential foraging) areas could be detected on visual inspection. Annual means of bathymetry, slope, SST and Chl *a* concentration associated with locations of Chatham Albatrosses within the 'high use' areas, differed significantly (test statistics given with Figure 3). On average, during foraging trips in 2007 birds concentrated at deeper waters and in areas with less slope than in 2008 and 2009 (Figure 3 A & B). Mean water depth ranged between 1615.8 ± 33.7 m and 913.8 ± 14.3 m, with birds on average frequenting deeper waters during the 2007 season and shallower waters in 2009 compared to the other two years, respectively (Figure 3A). Differences in mean bathymetries were less pronounced between 2007 and 2008 than between each of these two years and 2009. Mean slope associated with birds in 'high use' areas varied from 1.2 ± 0.1° and 1.6 ± 0.1° and was largest in 2009 and lowest in 2007. Here, differences in mean slope between 2009 and 2008 were less compared to those observed in 2007 (Figure 3 B). Mean water temperatures (SST) visited within 'high use' areas varied between 14.9 ± 0.1°C in 2008 and 15.6 ± 0.1°C in 2009, while mean temperatures frequented during 2007 were intermediate at 15.2 ± 0.1°C (Figure 3 C). The mean Chlorophyll a (Chl *a*) concentrations

associated with high densities of Chatham Albatrosses were much larger in 2007 with 1.1 ± 0.1 mg/m^{-3} than in 2008 (0.3 ± 0.01 mg/m^{-3}) and 2009 (0.6 ± 0.01 mg/m^{-3}; Figure 3 D).

The degree of individuality in habitat associations within 'high use' areas was high each year, with 70% of all individuals differing significantly ($p < 0.05$) from each other in terms of mean values of bethymetry, slope, SST and Chl *a* they were associated with. The five individuals which were tracked in two different breeding seasons showed little annual consistency, with mean values of the associated environmental characteristics varying significantly across years ($p < 0.001$), with the exception of one individual being consistent in terms of SST ($p = 0.26$) while another did not differ in terms of mean bathymetry associated with its potential foraging locations ($p = 0.27$).

Despite annual as well as individual variability, patterns in the environment frequented by foraging Chatham Albatrosses became apparent in each year of the study, which proved consistently different from that expected if birds were distributed randomly within their foraging range. The frequency distributions of habitat parameter values sampled within 'high use' areas differed significantly from frequency distributions sampled across the general foraging range on a random basis (test statistics given with Figures 4-7). Chatham Albatrosses were considerably more often associated with water depth below 1500 m and visited deeper waters (up to 5600 m) less than a random distribution would suggest (Figure 4). This pattern was found in each year of the study, although the distributions in 2007 and 2009 suggested a preference of waters less than 500 m depth, while in 2008 highest frequencies of bird locations were found at waters between 1000 m and 1500 m. The majority of slope values associated with both observed and randomly generated locations were below 4° in all three years of the study, indicating that very steep seafloor features were comparatively rare within the general foraging area (Figure 5). However, Chatham Albatrosses frequented areas of up to 15° slope within the 'high use' areas. In all three years, birds frequented comparatively steeper areas than suggested by the random distributions, but both types of distributions were most frequent at slope values below 1°. In terms of SST, Chatham Albatrosses again showed similar patterns in all three study years. Both random and observed bird distributions were skewed towards temperatures between 13°C and 18°C, but birds were found associated more frequently with temperatures of 14-16°C compared to random (Figure 6). Chl *a* concentrations within the general foraging area were generally less during the 2008 season than in 2007 and 2009, with maximum values of around 4 mg/m^{-3} compared to 10 mg/m^{-3} and 12 mg/m^{-3}, respectively (Figure 7). In 2008, birds exclusively

frequented areas with less than 1 mg/m^{-3} Chl *a*, but this did not deviate largely from what the birds would have done if distributed randomly. However, the tendency of the birds to associate with comparatively lower Chl *a* concentrations than according to a random distribution was apparent. Similarly, in 2009 both random and observed bird locations were found at Chl *a* concentrations of less than 2 mg/m^{-3}, and birds seemed to frequent areas of smaller Chl *a* concentrations more often than random. In contrast, during the 2007 season birds were more associated with higher and less with lower Chl *a* concentrations than would have been expected according to a random distribution (Figure 7).

Table 1: Number and duration of foraging trips of Chatham Albatrosses during early chick rearing in November/December 2007-2009. Track duration is given in days [d] and "-" indicates the recording of a track was incomplete. For birds which did more than one trip during logger deployment the durations for each track are given separated by "/".

Year	Bird ID	No. of tracks	Track duration [d]
2007	A02	1	3
	A03	1	2
	A04	1	3
	A05	1	3
	A07	1	2
	A08	1	3
	A09	1	2
	A10	1	3
	A11	1	3
	A12	3	2 / 2 / 2
2008	A02	2	4 / 2
	A03	1	-
	A10	1	4
	A11	2	1 / 3
	A14	1	3
	A15	1	2
	A20	2	3 / -
	A23	1	6
	A32	2	4 / -
	A34	1	3
	A81	1	6
	A82	1	6
	A94	2	2 / -
	A95	2	4 / -
	B00	1	-
	B11	1	3
	B12	1	5
	B17	1	3
	B35	1	4
	B37	1	-
	C03	1	3

Table 1. Continued.

Year	Bird ID	No. of tracks	Track duration [d]
2009	33852	1	3
	33853	1	-
	33859	1	3
	33877	1	5
	33894	3	1 / 1 / 4
	A05	2	4 / -
	A53	1	2
	A90	1	2
	B03	1	2
	C25	4	3 / 1 / 2 / 1
	C28	1	3
	C29	1	3
	C30	1	-
	C31	1	2
	C32	1	-
	C38	1	1
	C40	1	-
	C46	2	1 / 3
	Σ = 44 Ind.	Σ = 49 tracks	mean = 2.8 ±0.2 days

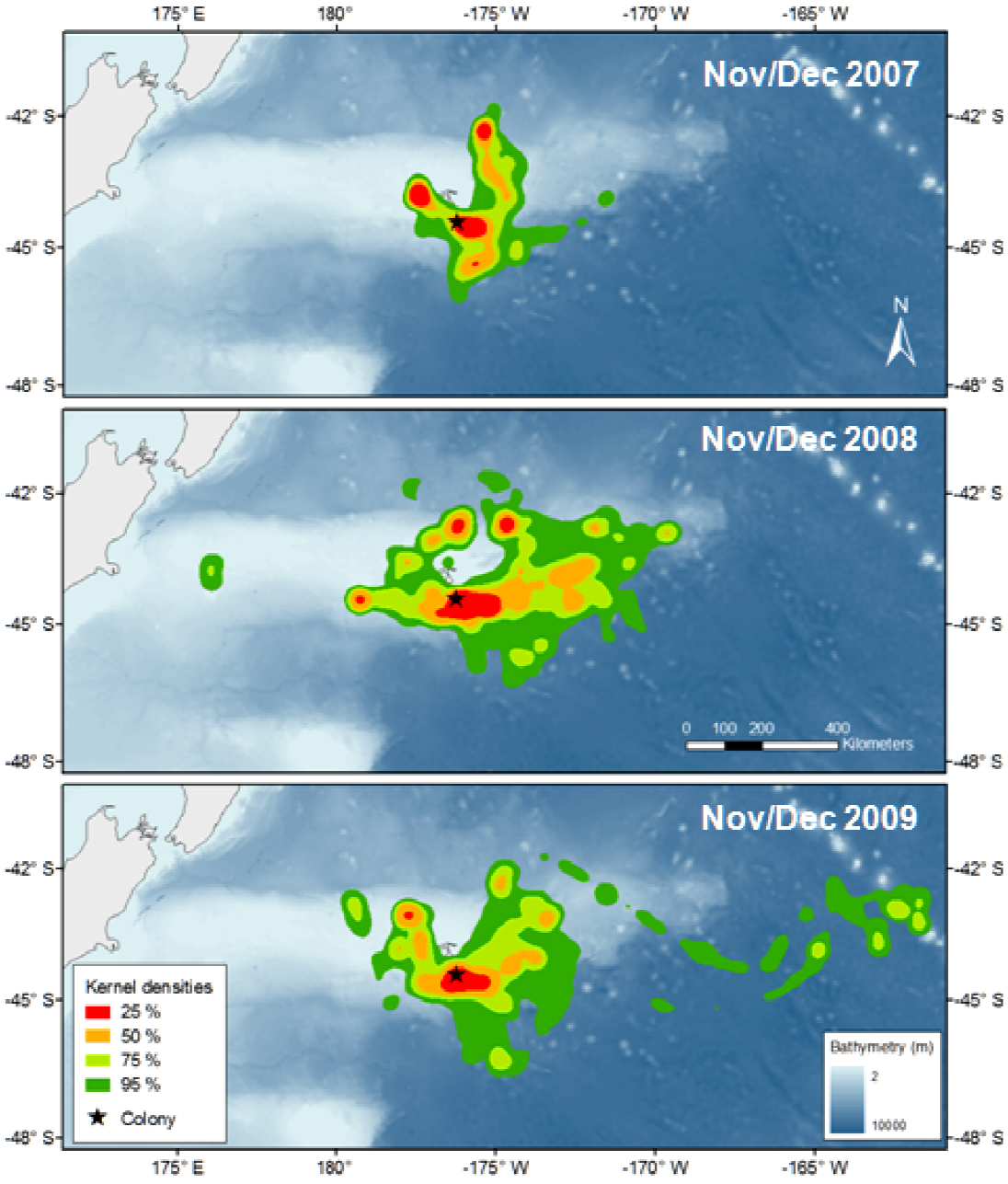


Figure 1: Spatial distribution of foraging Chatham Albatrosses during early chick rearing in November/December 2007 (A), 2008 (B) and 2009 (C) shown as kernel density estimates.

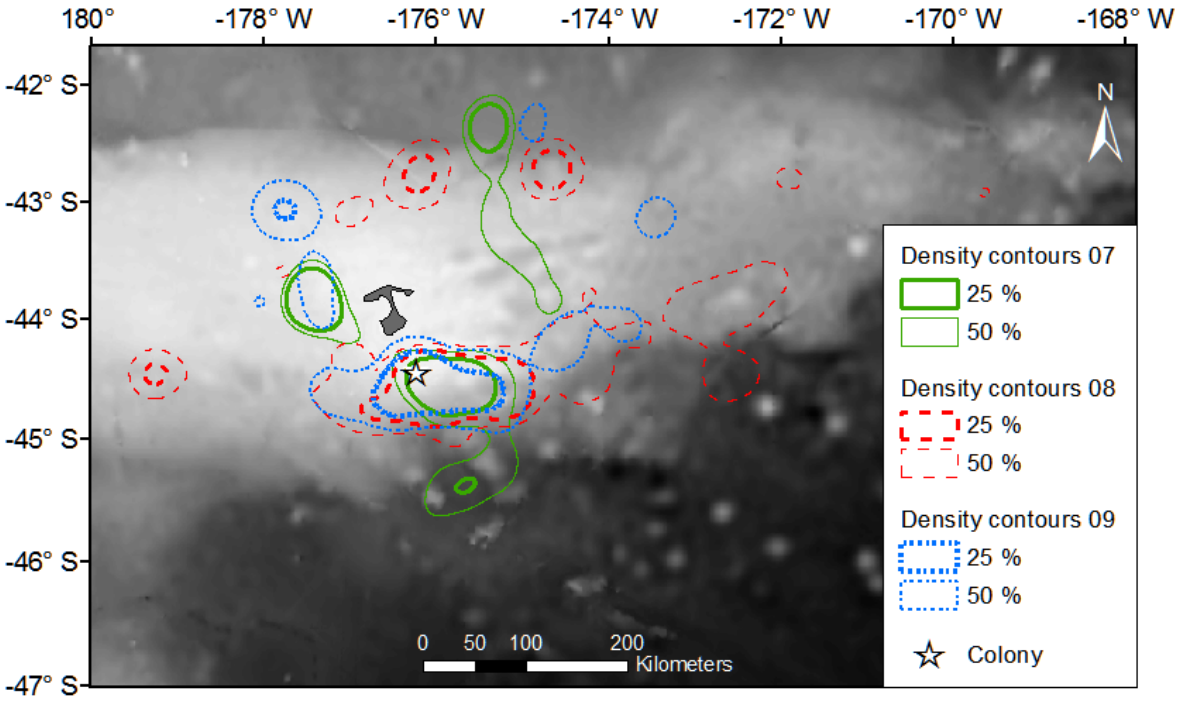


Figure 2: Spatial overlap of annual core areas in the general foraging distribution of Chatham Albatrosses during early chick rearing in November/December 2007-2009. Shades of grey describe bathymetry (darkening with increase in depth).

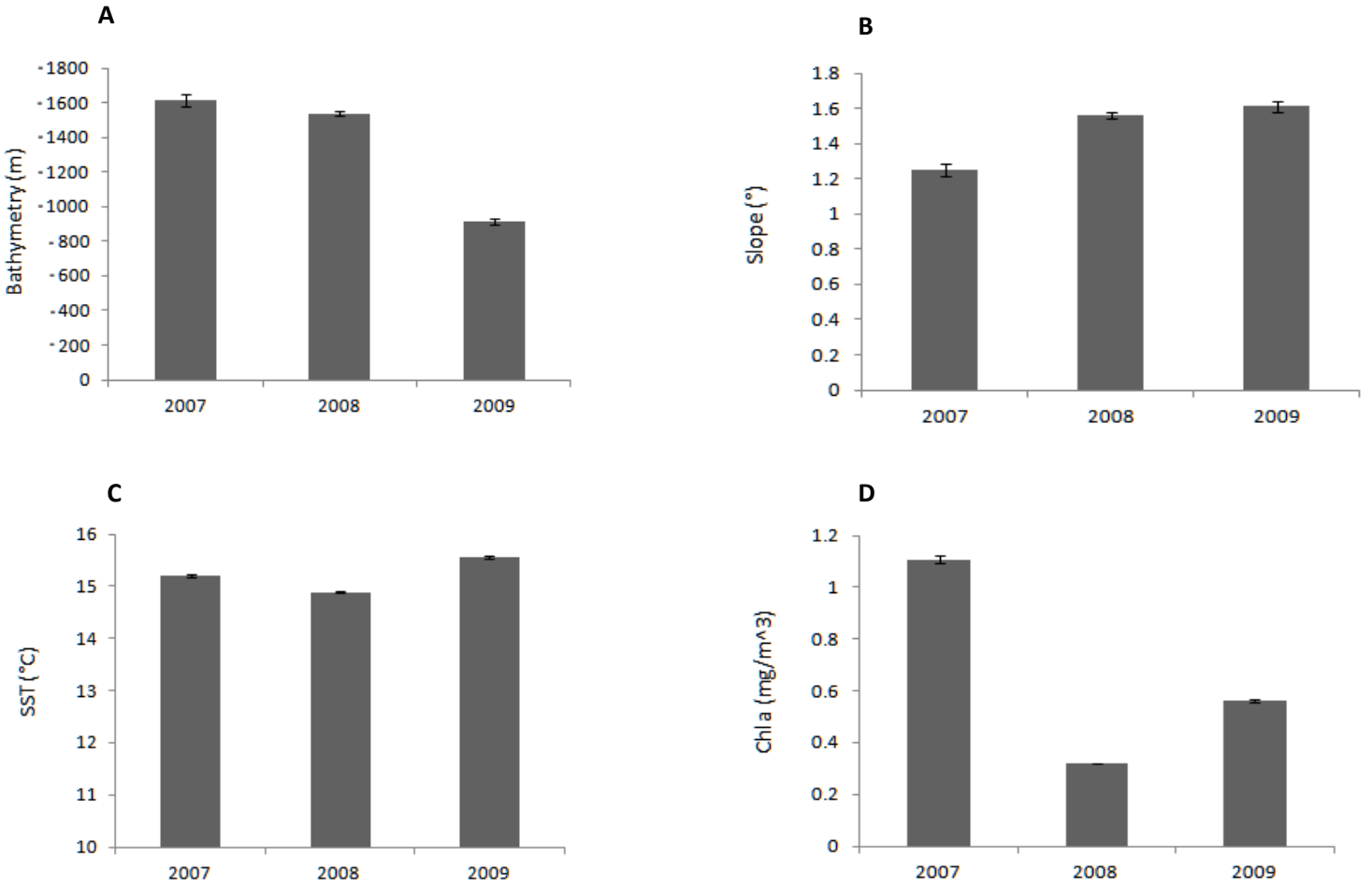
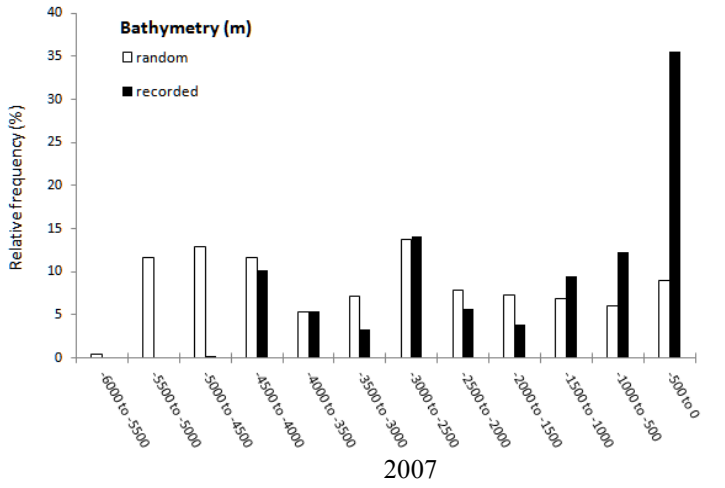
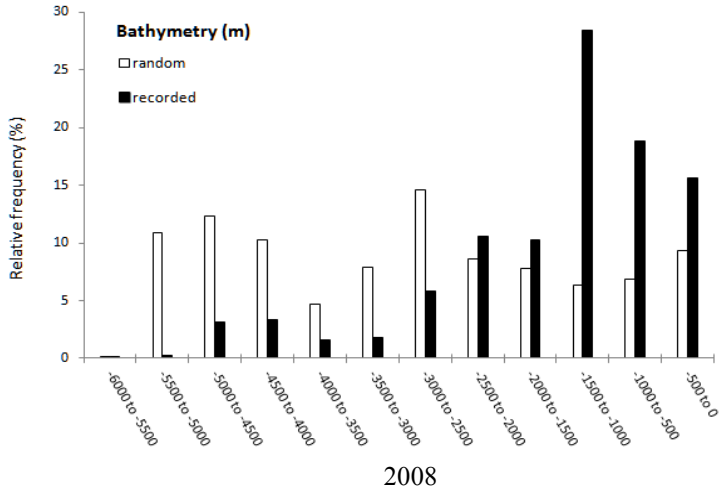


Figure 3: Annual mean values (± SE) of habitat parameters associated with Chatham Albatrosses within 'high use' areas on foraging trips during early chick rearing in November/December 2007-2009. Annual differences for each parameter were tested using GLMM with bird ID as random effect and proved to be significant at $p < 0.001$ level.



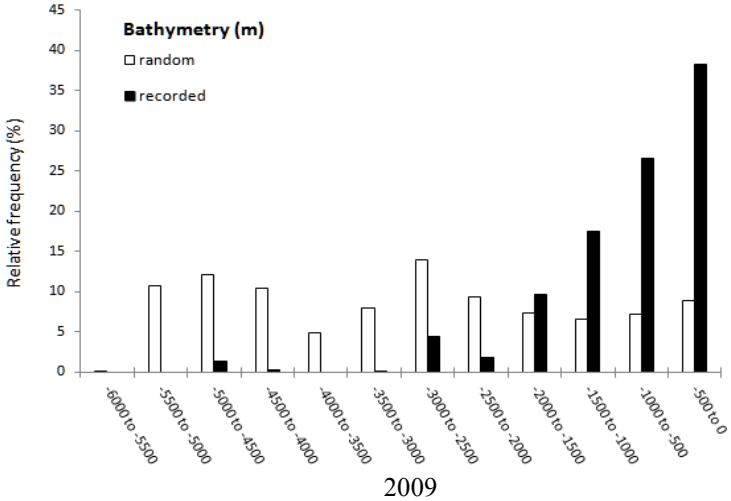
2007

KS-test: D = 0.36; p < 0.01



2008

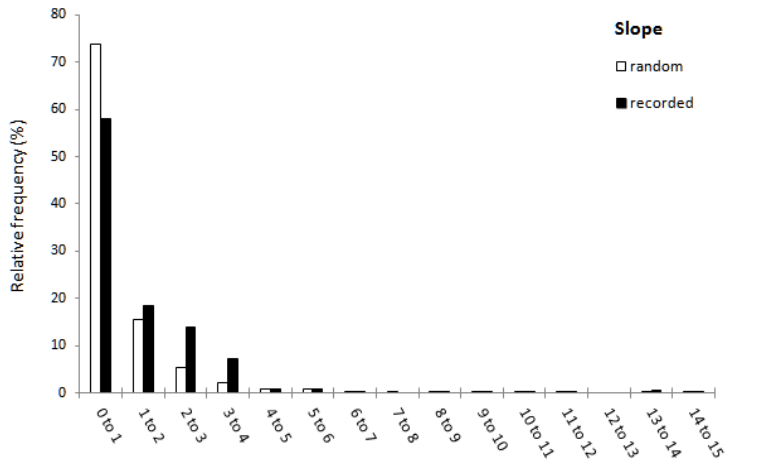
KS-test: D = 0.46; p < 0.01



2009

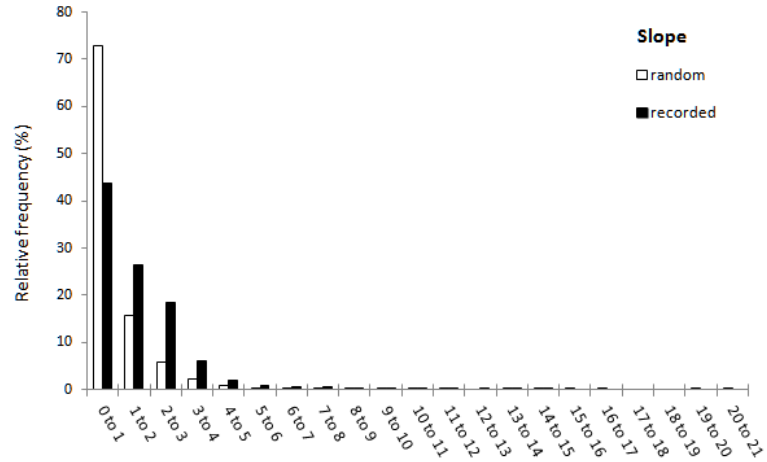
KS-test: D = 0.63; p < 0.01

Figure 4: Frequencies of bathymetry in association with recorded bird locations within 'high use' areas and random point distributions within the general foraging range of Chatham Albatrosses during early chick rearing in November/December 2007-2009.



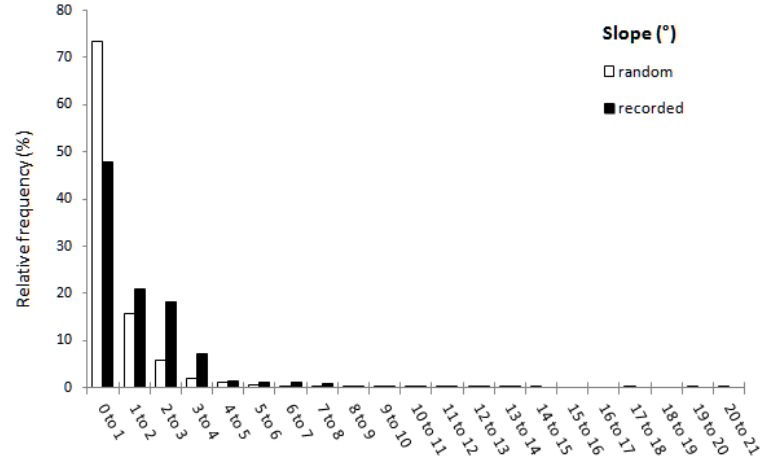
2007

KS-test: D = 0.16; p < 0.01



2008

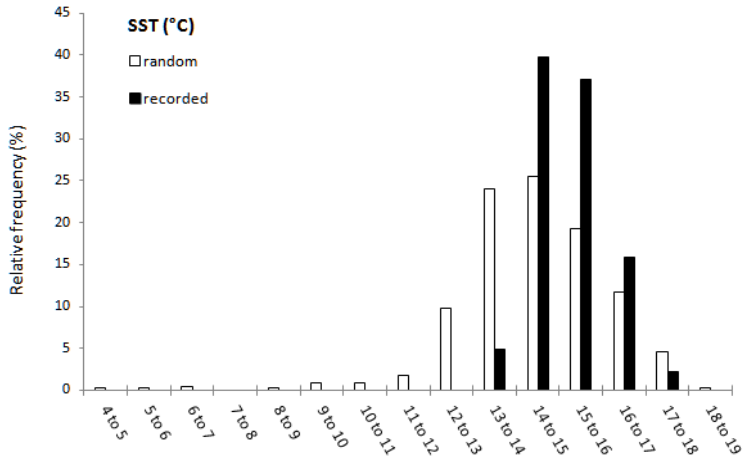
KS-test: D = 0.29; p < 0.01



2009

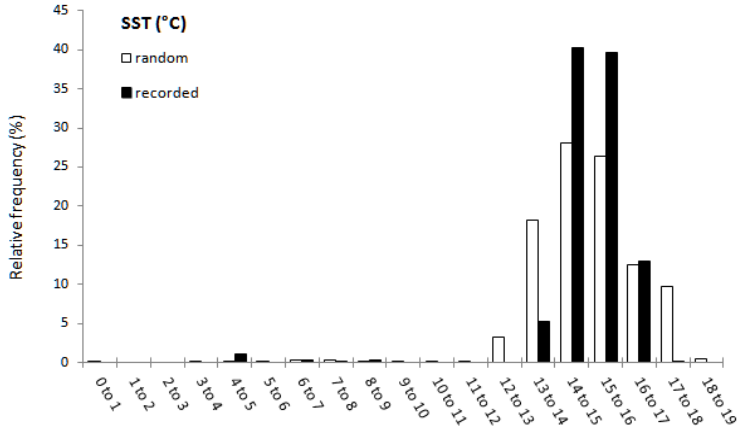
KS-test: D = 0.26; p < 0.01

Figure 5: Frequencies of ocean bed slope in association with recorded bird locations within 'high use' areas and random point distributions within the general foraging range of Chatham Albatrosses during early chick rearing in November/December 2007-2009.



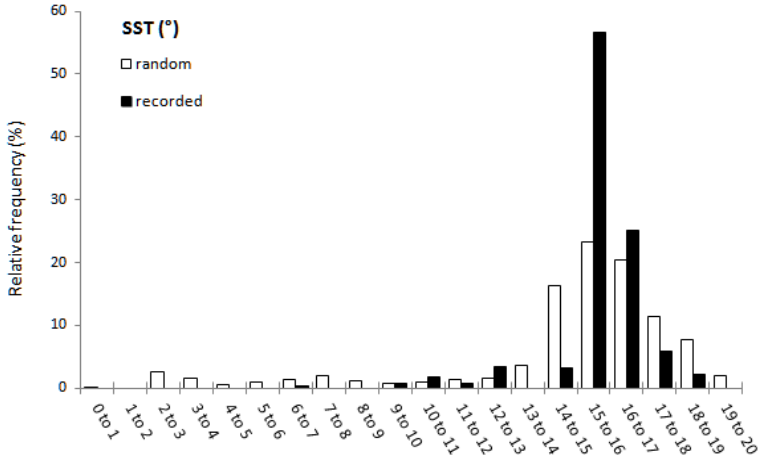
2007

KS-test: D = 0.38; p < 0.01



2008

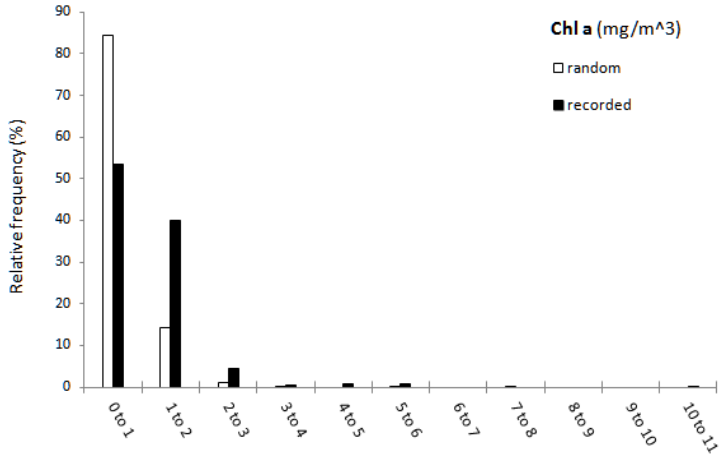
KS-test: D = 0.18; p < 0.01



2009

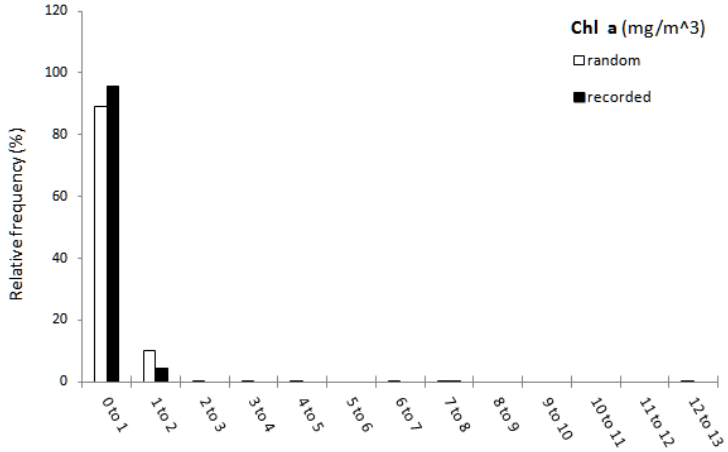
KS-test: D = 0.25; p < 0.01

Figure 6: Frequencies of sea surface temperature (SST) in association with recorded bird locations within 'high use' areas and random point distributions within the general foraging range of Chatham Albatrosses during early chick rearing in November/December 2007-2009.



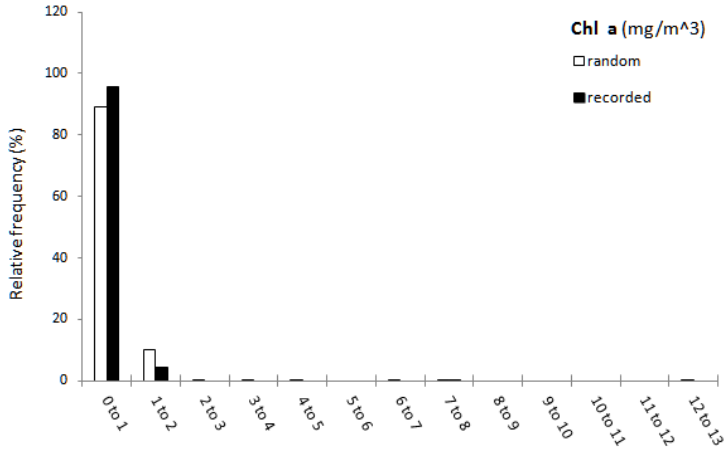
KS-test: D = 0.44; p < 0.01

2007



KS-test: D = 0.15; p < 0.01

2008



KS-test: D = 0.09; p < 0.01

2009

Figure 7: Frequencies of Chlorophyll a (Chl *a*) concentrations in association with recorded bird locations within 'high use' areas and random point distributions within the general foraging range of Chatham Albatrosses during early chick rearing in November/December 2007-2009.

DISCUSSION

Foraging range and trip duration

Chatham Albatrosses were found to remain within the shelf and shelf-slope area of the Chatham Rise during early chick rearing, and the extent of their general foraging range, apart from two outliers, did not exceed 400 km in all three years of the study. This agrees with findings from preliminary satellite tracking studies in 1997/1998, where birds were reported to generally range within 360 km of the colony whilst feeding chicks (Robertson and Nicholls in BirdLife International 2004). The foraging range observed during this study can be assumed to be their minimum range as albatross species increase their foraging range during chick rearing compared to other stages of the breeding period (Stahl and Sagar 2000; Hedd et al. 2001; Awkerman et al. 2005).

The restriction of foraging ranges to continental slope and shelf-break areas during chick rearing has been found in several other albatross species (Brothers et al. 1998; Cherel et al. 2000; Huin 2002; Nicholls et al. 2002; Troup 2004; Waugh et al. 2005). Bathymetric features are assumed to attract birds to these areas due to upwelling processes linked to increased productivity, and because they provide a predictable foraging environment (Cherel et al. 2000; Hedd et al. 2001). Birds are thought to be able to recognize shelf areas due to ocean colour or odours (Weimerskirch et al. 2007), and they often show high site fidelity to shelf waters, especially during chick brooding (Humphries et al. 2012). Contrasting foraging strategies are found in great albatrosses such as Wandering (*Diomedea exulans*) which despite increased energy expenditure range further into deep offshore waters, exploiting a pelagic habitat that is less predictable and where prey is distributed sparsely, reflected by birds rarely returning to the same foraging sites (Humphries et al. 2012). Though it might appear that differences in distribution and foraging strategy are size dependent, Nicholls et al. (2002) found differing foraging ranges in three great albatross species from different breeding sites (*Diomedea sanfordi* from the Chatham Islands, *D. antipodensis* from Antipodes Island and *D. exulans* from South Georgia), with only *D. sanfordi* being observed to not forage beyond the shelf and shelf-break of the Chatham Rise. Such behaviour indicates that foraging strategies in combination with habitat use during breeding are not just species specific but may also be related to the location of the breeding site. Wakefield et al. (2011) found little spatial overlap between the foraging ranges of Black-browed Albatrosses (*Thalassarche melanophrys*) from different colonies.

Chatham Albatrosses were consistent in their use of shelf and shelf-break waters over the three years of the study. The two individuals which travelled more than 400 km still remained either on the continental shelf or visited seamounts to the east which are also characterised by steep slopes. However, on a finer scale, high density areas (i.e., potential foraging locations) within the general foraging range of the species were found to be subject to annual variation. Only the intense use of the south-eastern shelf-break zone of the Chatham Rise was a temporally consistent pattern, confirming observations made in the 1990's (Robertson and Nicholls in BirdLife International 2004). The spatial distribution of the high density areas showed no clear preference for shelf or shelf break which may be related to the temporally and spatially mobile food sources the birds are pursuing. It is likely that foraging site preference includes not just prey items made available by certain environmental conditions, but also increased food availability due to commercial fishing operations in the Chatham Rise area. Torres et al. (2011) found that the locations of foraging trips in White-capped Albatrosses (*Thalassarche steadi*) were similarly quite variable and this variation coincided with the distribution of fisheries. Waugh et al. (2005) also found that hotspots of activity in foraging albatrosses coincided with the locations of fisheries. Track patterns described by Torres et al. (2011) as being indicative of following a fishing vessel (i.e., drift-like structures) have been found repeatedly in foraging tracks of Chatham Albatross on visual inspection. However, no corresponding analysis of these features was made in the current study and they might well result from current drift during surface feeding that is unrelated to fishing vessels.

Trip durations observed in Chatham Albatrosses did not exceed 6 days in the current study and individuals foraged for a maximum of 8 days according to satellite tracking in the 1990's (Robertson and Nicholls in BirdLife International 2004). Thus, the species does not appear to follow the pattern of alternating between short and long foraging trips during chick rearing as found for other albatross species (Stahl and Sagar 2000, Fernández et al. 2001). In *Pterodroma* petrels, Rayner et al. (2012) suggested that during energy demanding periods like chick rearing the time available at sea might determine distance travelled, more than habitat selection. In albatrosses it is assumed that shorter trips relate to the need of providing the chick with regular meals (Brothers et al. 1998, Hedd et al. 2001, Catry et al. 2004). The trip durations recorded for Chatham Albatrosses appeared to coincide with the general extent of their foraging range on an annual basis, with birds in 2007 doing more short foraging trips and ranging less far than in 2008 and 2009. However, theoretically birds could venture much

further than they actually did in up to 6 days. Remaining within a smaller range means that they could spend more time foraging and less on travel. This leads to the suggestion that the spatio-temporal pattern observed in brooding Chatham Albatrosses occurs because there is sufficient foraging habitat close by but a fairly small time window in terms of chick provisioning limits how long parents can be away from the colony.

Habitat selection in relation to environmental characteristics

Identification of potential foraging spots

To analyse habitat selection on a finer scale, and in relation to areas of specific importance (i.e., potential foraging spots), I focused on associations between bird locations and habitat parameters in 'high use' areas, which have been identified within the general foraging range of Chatham Albatrosses. Although it was assumed that 'high use' areas mainly result from birds actively searching for food or feeding, it is acknowledged that aggregations, based on which 'high use' areas were identified, might also result from other behaviours causing birds to spend extended periods of time within one place, e.g. socialise, groom, rest and/or sleep. Torres et al. (2011) assumed that 'drift points' (very little speed along straight path) within GPS tracks of White-capped Albatrosses (*Thalassarche steadi*) were related to resting rather than foraging and thus they were excluded from the analysis of potential foraging points. However, sitting on the water without moving could also indicate foraging or feeding according to the 'sit and wait' technique (Weimerskirch et al. 2007).

Potential drivers of habitat selection during foraging

To identify patterns in habitat use during potential foraging events (i.e., bird aggregations in 'high use' areas), I investigated two spatially and temporally fixed (bathymetry and slope) and two environmentally variable habitat parameters (SST and Chl *a*) and could show that the identified associations with certain characteristics of these habitat parameters were different from random. This was true for each year of the study and suggests that despite considerable degrees of annual as well as individual variability, the occurrence of potential foraging events in chick-rearing Chatham Albatrosses is related to distinct patterns of bathymetry, slope, SST and Chl *a*. The overall pattern of birds foraging in comparatively shallow waters but at the same time being associated more often with steeper slopes than expected, mirrors the restriction of the general foraging range to mainly shelf and shelf-slope areas. Given the static nature of these two habitat parameters, annual differences of habitat choice have to be attributed to other factors or to individual variability in the fine scale

distribution of foraging locations, i.e., the lack of commonly used foraging areas by the species. It is not quite clear however, whether annual as well as individual differences in mean SST or Chl *a* concentrations in association with potentially foraging birds result from differences in the distribution of these parameters across the birds' foraging range each year or to the fact that individuals did not come back to the exact same foraging location. Tests for annual differences in the habitat preferences of the same individuals, resulting in little consistency across years, prove that habitat preferences are less likely to be detected on an individual level than on a species level.

All four habitat parameters investigated in this study at least partly explained the location of potential foraging spots, but habitat selection within those 'general brackets' was subject to individual as well as seasonal variability. In terms of SST it has to be noted that this bracket was fairly narrow, with most birds associated with 14-16°C waters and mean annual differences being less than 1°C. Although statistically different, it is questionable whether such differences are biologically significant (i.e., related to differences in food availability). Hedd et al. (2001) observed that brooding Shy Albatrosses (*Thalassarche cauta*) exploited consistent temperature ranges within their foraging habitat and proposed this reflected consistent patterns of prey availability. In Waved Albatrosses (*Phoebastria irrorata*), Awkerman et al. (2005) found that SST and Chl *a* at least partly explained habitat use during foraging. However, these parameters proved to be less consistent in providing clear patterns compared to bathymetry. The link between habitat features and food availability is also suggested by the pattern observed between Chatham Albatross locations and Chl *a* concentration. Birds frequented comparatively more productive regions (as determined by Chl *a* concentration) within their 'high use' areas than random, but these differences did not seem strong during the 2008 and 2009 seasons. However, in 2007 this pattern became clearer. These annual differences are probably beyond what could be explained by individual variability. A possible explanation would be that a strong La Niña in 2007 concentrated food resources (http://www.cpc.ncep.noaa.gov/products/analysis_monitoring/lanina/cold_impacts.shtml). That Chl *a* is only a rough estimate of food abundance for species higher up the food chain, is illustrated by Freeman et al. (2010) who found significant relationships between foraging movements and regions of the shelf break in Black Petrels (*Procellaria parkensoni*), but relationships with Chl *a* did not prove to be significant despite the assumption that upwellings and high productivity are associated with respective areas.

Conclusions

In the study presented here, I was only able to investigate the distribution of foraging Chatham Albatrosses in relation to a few environmental variables for which information of sufficient detail was available. It has to be acknowledged that these variables are only related to albatross distribution indirectly (via a number of intermediary steps influencing the distribution and availability of prey), which is particularly true for Chl *a* concentrations, and it is thus not surprising that the observed patterns in habitat choice were variable. Moreover, additional factors may need to be taken into account to get a more comprehensive picture on how the observed patterns in foraging habitat selection can be explained. No doubt, there are a number of other environmental variables that may play an important role in determining where and for how long a bird travels when on a foraging trip. For example, Suryan et al. (2006) considered wind as a potential factor for foraging distribution, as they found Short-tailed Albatrosses (*Phoebastria albatrus*) concentrated in areas of low winds. The tracking of fishing vessels as observed by Torres et al. (2010) in White-capped Albatrosses is another possible factor to influence foraging distribution.

Despite my inability to identify the exact determinants governing the movements of Chatham Albatrosses, my results support the hypothesis that this species is not choosing their foraging habitat randomly and I presume that this is due to some sort of active choice behaviour. It is quite likely that they may be opportunistic in responding to a number of different cues offered within their foraging environment. The observed annual and individual variability in foraging distribution and habitat selection of Chatham Albatrosses may indicate that important marine areas for highly mobile species like albatrosses are not fixed but vary at a finer scale according to changes in the dynamic marine environment. As Cherel et al. (2000) suggest, albatrosses probably rely on resources that are roughly predictable in location, but whose availability nevertheless varies from one year to the next. It is the dynamic nature of their foraging habitat that will be both challenging to understand and to preserve.

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CHAPTER 5

Conclusions

In this thesis I investigated the spatial and temporal patterns in the at-sea distribution of three threatened or near-threatened New Zealand endemic albatross species (Chatham Albatross, Northern Buller's Albatross and Northern Royal Albatross) and their habitat use in relation to behavioural and physical processes. Movement patterns and habitat use were studied during three stages of the annual life cycle (breeding, migration and non-breeding) and I identified potential mechanisms driving the distributional behaviour of the species.

In **chapter 2**, I showed how the three study species segregate temporally and spatially within their non-breeding grounds off the South American coast. I identified the species-specific high density areas within the region and concluded that these are southern Peruvian waters in the Chatham and Northern Buller's Albatross, and southern Chilean waters and the southern part of the Patagonian shelf in Northern Royal Albatrosses. I showed how each species spent different periods of time within South American waters, and demonstrated how the birds moved within their general non-breeding ranges on a finer scale, leading to a more comprehensive and detailed picture on how the species used their habitat over time, such as the directed northward movement of Chatham and Northern Buller's Albatross. SST (as a proxy for prey availability and distribution) appeared to be a major driver for the observed movements, as the birds moved in concordance with the shift of distinct oceanic temperature regimes. Moreover, the spatial segregation observed between the two members of the genus *Thalassarche* (Chatham and Northern Buller's Albatross) and the larger species of the genus *Diomedea* (Northern Royal Albatross) within waters of different temperatures is likely based on differences prey preferences amongst species.

In the next two chapters, I investigated the routes, duration and activity patterns on migration (**Chapter 3**) and the foraging range as well as the distribution of potential foraging spots in relation to different environmental characteristics during breeding (**Chapter 4**) in Chatham Albatrosses over consecutive years. This gave me the opportunity to identify whether the species remained consistent in terms of habitat selection and use. I found that birds did not simply traverse the South Pacific when moving between breeding and non-breeding grounds, but stopped to exploit temporal feeding opportunities within their migration habitat, possibly generated by frontal systems. This pattern, as well as the route followed on migration, was persistent across years. During chick-rearing, birds remained within the area of New Zealand's extended continental shelf, the Chatham Rise, and did not venture further into pelagic waters. Within this range, no common or recurring areas of generally high bird densities could be detected, other than a small area in the vicinity of the

species' breeding colony (The Pyramid) close to the southern shelf edge. The occurrence of potential foraging locations appeared to follow patterns in bathymetry, slope, SST and Chl *a* features within the region, but was subject to a high degree of variability in the actual location across years on a fine scale. Differences among individuals seemed the source of most variance in parameters like the timing of departure and arrival dates, duration of migration and duration of stopovers, and also in the location of potential foraging spots during breeding. However, the degree of individual variation itself remained consistent across years and might thus be regarded as species-specific.

Since the scope of my thesis was to explore the spatial and temporal dynamics of New Zealand albatrosses from a conservation perspective (due to the funding body being the Ministry of Fisheries and all study species are subject to the NPOA-Seabirds; Taylor 2000), the following concluding discussion is focussed on issues dealing with the conservation applications of the results presented in the previous chapters. Possible interactions with commercial fisheries are discussed as well as contributions to the identification and implementation of candidate sites to be considered in future conservation planning.

For similar reasons, the analytical approaches in my research were chosen to address questions on the population level, to create a comprehensive picture of basic patterns and processes according to which the study species are distributed. This is regarded as fundamental before addressing further issues or evolving questions following individual-based approaches (as mentioned in Wakefield et al. 2009).

Interactions between Albatrosses & fisheries

A major part of the marine areas used by the albatross species I studied coincided with areas also intensely used by commercial fishing operations (i.e., Chatham Rise during breeding; Humboldt Current and Peruvian shelf and Patagonian shelf areas during non-breeding).

According to maps published in Tuck (2004), demersal fishing effort appears to be comparatively high in the Chatham Rise, however, the data are too coarse to identify overlap with the foraging ranges identified for chick-rearing Chatham Albatrosses at a finer scale. Baird et al. (2011) reported that most of New Zealand's trawl effort occurs in waters shallower than 800 m and that 33% of effort was made in areas including the Chatham Rise. This corresponds with the preferred water depths I identified for foraging Chatham Albatrosses during breeding, suggesting a high potential for overlap between fisheries and the preferred habitat of Chatham Albatrosses. Similarly, longline fishing effort within the region

of the Peruvian shelf, as documented in ACAP (2008), appears to be highest during April to September, which corresponds to the time that Chatham Albatrosses as well as Northern Buller's Albatrosses were recorded in this area, and which coincides with the areas of highest density for both species. Increased demersal fishing effort is also reported for southern Chilean waters and the southern Patagonian shelf (PEW longline report), which overlaps with the non-breeding distribution found for Northern Royal Albatrosses. It has to be noted though that data on fishing effort is often incomplete, if not missing altogether due to inconsistent reporting (G.N. Tuck, pers. comm.) and thus identifying or even quantifying overlap between albatrosses and fisheries, especially on finer scales, is challenging.

In general, fisheries are viewed as detrimental to all albatross species, as they often perish as incidental bycatch (Robertson et al. 2003b). All three study species have been reported as being killed in commercial fishing operations in New Zealand waters (Conservation Services Programme. 2008; Murray et al. 1993; Robertson et al. 2003; Waugh et al. 2008), and both Chatham and Northern Buller's Albatrosses have also been recorded as incidental bycatch off Chile and Peru (BirdLife Global Seabird Programme 2008; Gales 1998; Robertson et al. 2003b). For Northern Royal Albatross no bycatch mortality has been reported for both the Chilean and Argentinean non-breeding areas (BirdLife Global Seabird Programme 2008; Favero et al. 2003). In all three species, bycatch is reported only as "occasional", but it is not clear whether this is due to a low susceptibility for this sort of fisheries interaction or if it instead reflects the generally low population numbers (as reported in Chapter 1).

Apart from direct mortality, commercial fisheries pose a further threat to albatrosses (and other seabirds) through the fact that they both exploit the same resource (Pichegru et al. 2009), which may result in a shortage if not depletion of food resources for the birds. A possible solution to mitigate overfishing is the implementation of 'no-take' zones in areas on which seabirds rely for foraging. Pichegru et al. (2012) found evidence that such areas make sense when they are large enough, and also include buffer zones to prevent fisheries from 'fishing the line' (i.e., skimming off fish overspill along the reserve boundaries) which can prevent fish stocks recovering. Apart from directly conserving food resources, 'no-take' or fishery exclusion zones could be beneficial to albatrosses by reducing the risk of bycatch in these areas and during times when the pressure to find food is high. However, as albatrosses also scavenge for food, fisheries cannot solely be regarded as a threat but also have to be considered as a potential beneficial factor affecting their distribution (Tuck et al. 2003). By

making more food available which would be either out of reach for albatrosses (e.g., trawl fisheries) or not there at all (e.g., bait on hooks for longlining), fishing operations indeed have the potential to attract the birds and provide them with more food than would otherwise be the case. Torres et al. (2011) showed in a study on White-capped Albatrosses and their potential overlap with fisheries that the birds appeared to track fishing vessels during parts of their foraging trips, presumably to take advantage of the food available. Considering these circumstances, 'no-take' zones may not work in terms of reducing the risk of mortality in fishing operations, since birds could be simply 'lured' out of a proscribed reserve through attraction to fishing vessels in the vicinity. Whether and to what extent the presence of fishing operations plays a role as an 'environmental factor' in the distributional patterns of albatrosses I observed in my studies, has yet to be determined. Following fishing boats might not be a detectable pattern on a larger scale like the one I was able to analyse for non-breeding species along the South American coasts, but could well be influencing the observed patterns on a finer scale, such as I studied during the breeding season of Chatham Albatrosses, where the individual as well as annual variation in foraging locations may be partly explained by the birds following fishing vessels. Nevertheless, little is known about the behaviour of Chatham Albatrosses towards fishing boats and any conjecture about the role of fisheries in the distribution of Chatham Albatrosses has to be left subject to future investigations. In any case, and as suggested by different authors (e.g. Pichegru et al. 2012, Garthe et al. 2012), fisheries would need to be managed at a larger scale apart from actual site protection. The extensive implementation of best fishing practice as in applying suitable mitigation measures (Løkkeborg 2011) to reduce or even prevent seabird bycatch in both national and international fleets, may be the more sensible course of action at present, and is a goal which hopefully can be achieved to ensure albatross conservation independent from boundaries.

Important areas for albatrosses at sea – site identification & implementation

One of the main objectives for studying the spatial and temporal distribution patterns of New Zealand albatrosses was to inform conservation planning in terms of the occurrence of important areas for these species throughout the year, and to provide a baseline from which to create a comprehensive network of 'candidate sites' for future protected and/or managed areas.

In the marine environment, the criteria to qualify as an 'important bird area' (IBA; BirdLife International 2010), which could be the first step towards site protection, are the number of individuals found at a certain site and whether the site its regularly used (BirdLife International 2010a; IBA category A4*ii*: "Site known or thought to hold, on a regular basis, ≥ 1% of the global population of a congregatory seabird"). These could either be seaward extensions of breeding colonies, non-breeding aggregations in coastal waters, areas of migration bottlenecks or, in case of pelagic species like albatrosses, marine areas remote from land which usually coincide with specific oceanographic features (Osieck 2004). IBAs are usually identified on a species by species basis (BirdLife International 2010a).

Gathering data for a sufficient number of birds to provide the information needed to confidently identify an IBA is a problem inherent to most tracking studies (BirdLife International 2010a). However, in my multi-year study on Chatham Albatrosses I was able to track a total of 45 birds, both at their breeding ground and during the non-breeding season, which, given the species' small population size (< 5000 breeding pairs; see chapter 1), meant that I had information on almost 1% of the breeding population. Accordingly, both the foraging range during chick-rearing of the species as well as their migration habitat that I recorded was based on reasonable numbers of the population. Since the birds were also found over three consecutive years to consistently occupy within same foraging range during brooding as well as frequenting the same migration corridor, results that are backed up by preliminary tracking studies in the 1990s (BirdLife International 2004; Nicholls and Robertson 2007), it seems safe to refer to these areas as regularly used and thus qualifying as IBAs.

The extent of IBAs around breeding colonies have been usually identified via a default 'foraging radius' based on foraging distances (BirdLife International 2010a), which more often than not led to seaward extensions being too small (Adams et al. 2012; Ludynia et al. 2012) and/or the inclusion of unused habitat (Thaxter et al. 2012). The marine IBA toolkit (BirdLife International 2010a) explicitly suggests that, "Ideally, remote-tracking of an adequate sample of individuals [...] should be carried out over several years to identify the most important areas".]. My study of Chatham Albatrosses meets this criteria fairly well, and on a mesoscale, has identified a more realistic extent of the Chatham Albatrosses general foraging range, or at least an area were the ranges of all three years overlap, compared to a default foraging radius. The area I defined as being used by Chatham Albatrosses could be brought forward as a candidate site for an IBA. The fact that the identified area is

characterised quite clearly by permanent oceanographic features (i.e., the shelf and shelf break area of the eastern Chatham Rise could facilitate delineation. The skewed shape of the general foraging range, stretching out far more to the east than to the north, south and west of the colony, is already much more informative than simply drawing a circle of 400-600 km radius, which in this case would include a good proportion of pelagic waters beyond the shelf edge, into which brooding Chatham Albatrosses only rarely ventured. However, arguing that the entire area should obtain protection status would be very hard, especially to exclude one of the main New Zealand trawl and longline fisheries from one of their main areas of use. Identifying smaller, more localised areas as a second option (i.e., protection of just part of their range) would at least for now prove challenging, since no clear spatial or temporal patterns (which would warrant 'regularity') could be detected on a fine scale in my study. The only area nearly in compliance with this particular IBA criteria would then be a zone to the south-east of the breeding colony, which again would be comparatively small and not representative given the spatial extent of foraging trips in general (see chapter 4). It also has to be noted that only data from the early chick-rearing period is available as a basis to identify important areas during breeding for this species. Knowing that many albatross species extend their range during incubation as well as post-guarding (Stahl and Sagar 2000; Fernández et al. 2001; Baduini and Hyrenbach 2003), the area identified in my studies might already be the minimum range. If it was a general preference of the species to forage over shelf and shelf break, the range observed might have not been restricted due to breeding status and would stay the same throughout the whole breeding season. As a result, given the uncertainties over which areas should be protected, the best scenario might instead (especially in respect of all species of albatrosses and other seabirds) be the implementation of better and more extensive bycatch mitigation measures in the existing fisheries throughout the Chatham Rise.

BirdLife International (2010a) states that in regard to IBA studies based on tracking data, activities during the time at sea, including feeding, travelling, roosting, resting and courtship, may all render respective areas suitable for inclusion in the IBA network. The general focus however has been on feeding areas as priority sites, linked to energy acquisition. Camphuysen et al. (2012) also stress the point that additional knowledge on behaviour at sea (or how an area is used) can aid in identifying the ecological relevance of a candidate site. This supports the assumption made in chapter 3, that the migration habitat of Chatham Albatrosses (i.e., high seas of the South Pacific), which the birds not only traverse on a

regular basis (along the same mean latitude of 40°S over consecutive years) but according to activity studies also use as a foraging habitat, is of importance for the species at that stage as it relates to energy gain. Its importance is further highlighted by the fact that a period of presumably energetically demanding migration follows on straight after a similarly energy demanding breeding season. Thus, although the criteria of regularity and relevance may be met in an IBA based on a migration corridor, the spatial constitution of important areas within this range does not appear to be possible due to the rather opportunistic manner in which birds were assumed to exploit frontal systems along their migration pathway (see chapter 3).

My study on non-breeding sites of three different albatross species as presented in chapter 2, probably lacks sufficient sample size per species as well as information on regularity of habitat use in terms of meeting IBA criteria. However, data sets like this are regarded as 'supplementary' and can still form stronger cases when combined, as for Chatham and Northern Buller's Albatross which both frequent Chilean and Peruvian waters at similar times and overlap in their overall high density areas on the Peruvian shelf. Accordingly, the area can be classified as a candidate site with IBA status pending the addition of supportive data (BirdLife International 2010a). What is also of interest in this study (chapter 2), apart from the general site identification, is the fact that birds follow distinct movements within generally important areas, which, especially in combination with the knowledge on the drivers of such habitat use (e.g., SST), can provide more detailed information on what section of an area becomes important at a given time for one or more different species. Accordingly, the extent of a protected and/or managed area might become smaller compared to the formerly identified area of 'general use' but at the same time would need to have shifting / temporally flexible boundaries. Smaller sites are usually easier to implement and as a result are preferred by managers and legislators (Lascelles et al. 2012). Figuring out how to deal with flexible or dynamic boundaries, however, is challenging but at the same time urgently needed (Lascelles et al. 2012; Louzao et al. 2012) in the marine habitat where birds, resources and even threats (e.g. fisheries, oil pollution, plastic debris) are mobile. One approach might be the design of a network of sites which boundaries are fixed (as in mapped precisely on official marine charts) but which could be 'switched' on and off according to the times of high use by seabirds within respective areas.

Oceanic features (e.g. SST, bathymetry, slope, Chl *a*), as I investigated as possible 'drivers' or explanatory factors for observed bird distributions, could also aid in the

delineation of boundaries for marine protected areas. Such habitat suitability analyses are already used within the IBA identification process (BirdLife International 2010a). Again, only the static parameters like bathymetry are straight forward in this respect, while seasonally changing variables like SST require flexible and thus more advanced approaches (Arcos et al. 2012).

Apart from the designation of actual boundaries, another important point is the need to predict (or at least monitor) potential shifts or relocations of seabird distributions under changing climatic conditions once knowledge about 'what drives habitat choice' is achieved (Grémillet and Boulinier 2009). Such changes are usually expressed by changes in temperature. In my studies presented in this thesis, I found SST in particular an important and fairly consistent parameter in explaining the distributional patterns of the albatross species observed, as it became apparent in all three stages of the annual cycle. During breeding, the foraging locations of Chatham Albatrosses were associated with at least similar SST ranges each year, despite the seasonally flexible nature of this parameter. While on migration, again a connection to certain ocean temperature regimes was observed, although more indirect, when birds moved along and exploited frontal systems while crossing the South Pacific transition zone between subtropical and subantarctic frontal systems, where warm and cold water masses meet and resulting processes possibly create foraging opportunities for migrating Chatham Albatrosses. And lastly, during non-breeding, all three species of albatrosses were observed to spatially segregate according to processes related to certain SST ranges, as well as move in concordance with temporal shifts in local temperature regimes. More work needs to be done to examine the link between SST and how birds select their habitats, but this feature at least appears to be a good place to start in exploring how it could be used to better manage threats to albatrosses throughout their life cycle.

Recommendations for further research

The research presented here was conducted to improve upon our previously limited knowledge on the three rare or uncommon albatross species studied to enable conservation measures to be implemented. Although several aspects of the distribution, movements and behaviour of Chatham, Northern Buller's and Northern Royal Albatrosses have been elucidated by my work, more detail awaits to be discovered, and much of my work may be regarded as a baseline study for future research, which, as so often happens with biological research, leads to more questions raised than have been answered.

Although in the previous sections I outlined, what I believe to be valid conservation applications derived from my work, these are just the first pieces to the puzzle on how the sites identified as important for my study species function in their entirety, both in respect of other seabird species using such areas at the same or different times of the year, and in terms of further exploration of the environmental factors which 'set the scene'. The non-breeding sites that the three study species occupy off South America are also used to a certain extent by a variety of other seabirds, including Southern Buller's (*Thalassarche b. bulleri*) and Salvin's Albatross (*Thalassarche salvini*), Chatham (*Pterodroma axillaris*), Westland (*Procellaria westlandica*), and Cooks Petrels (*Pterodroma cookii*), and Sooty Shearwaters (*Puffinus griseus*; Shaffer et al. 2006; ACAP 2008; Landers et al. 2011; Rayner et al. 2011; Rayner et al. 2012; P. Sagar, pers. comm.), which all similarly migrate from New Zealand, as well as Wandering (*Diomedea exulans*), Black-browed (*Thalassarche melanophrys*), Waved (*Phoebastria irrorata*) and Grey-headed (*Thalassarche chrysostoma*) Albatrosses and White-chinned (*Procellaria aequinoctialis*) and Giant Petrels (*Macronectes halli* and *giganteus*), migrating from elsewhere or resident (ACAP 2008; González-Solís et al. 2008; Quintana et al. 2010). This includes only some of the Procellariiformes, and the area is important to a variety of other seabirds, including terns, gulls, cormorants and boobies. Similarly, on the Chatham Rise area where the study species forage whilst breeding is also used by Southern Buller's and Salvin's Albatross, Chatham, Westland, and Cooks Petrels, and Sooty Shearwaters, but also White-capped (*Thalassarche steadi*) and Antipodean Albatross (*Diomedea antipodensis*; ACAP 2008, 2011; and see references above) from New Zealand breeding populations. To determine how all these species interact on both spatial and temporal scales, when they arrive and depart, how long they stay, to what extent they overlap in space and time is of conservation interest. This information can then be used to define IBAs and eventually protected sites on a much more holistic and thorough level. BirdLife International and its regional partners are already working on these topics, making use of the extensive 'tracking data base' (http://www.birdlife.org/ community/2010/09/the-global-procellariiform-tracking-database/), to which my work has and will contribute. It will be interesting to investigate for example, as to whether the movement patterns I found for Chatham and Northern Buller's Albatross within the Humboldt Current System can be observed for other species using the same area or how diverse the habitat use will be given different biology, behaviour and annual schedules of the species mentioned above. It will also be interesting to see if the idea of having the whole Peruvian and Chilean coast as one big

IBA or protected area is favoured or instead, a sequence of smaller sites according to species-specific graduation in time schedules is implemented. To me the latter makes more sense but sometimes one simply aims for most obvious common grounds.

For the conservation of any species of seabird, including the three species of albatross I studied, it will be important to study birds at different stages in their life cycle, i.e., learn more about the distributional patterns of not only breeding birds but also non-breeders and immature birds, which for many species comprise a considerable proportion of the population. This is especially true in albatrosses and other Procellariiformes where birds take about 5 years before they start to breed, and they hardly ever come ashore during that time (Warham 1990; Weimerskirch et al. 2006). Better knowledge on how these birds fare while out at sea and their probability for survival under different environmental conditions and at different stages of their life cycle, would considerably improve our ability to estimate the population as well as conservation status of a given species. Depending on site accessibility and project funding, enabling researchers to stay on breeding islands long enough to reach different age classes, as well as apply transmitting rather than logging devices, some studies already currently exist on the potentially different distributional patterns of juveniles or non-breeders (Walker and Elliott 2006; Weimerskirch et al. 2006; Phillips et al. 2008; Thomas et al. 2010). However, due to limitations of both current logging and transmitting devices the full period between fledging and first time of breeding has not yet been studied (Thomas et al. 2010). GLS devices have the advantage in that they last long and are easy to attach but loggers would be hard to retrieve from birds who never had established a nest site before and whose return time can only be roughly estimated. Unfortunately, currently available GPS transmitters have too limited a battery life to stay on an immature bird for several years. Moreover, the size and weight of the transmitters does not allow for easy attachment on a leg band and thus has to be either taped onto feathers (and thus gets lost at the next moult) or attached via harness, which is thought by some researchers to be detrimental to albatrosses, as well as a variety of smaller species (Phillips et al. 2003). However, the current pace of miniaturization and further development of tracking devices gives hope that answering such questions will not lie in the too far future. In this respect it would be also desirable to revisit distributional patterns during the non-breeding season on a finer scale to get more detailed information on the actual habitat use by birds along the South American coastline. This will help us make yet better informed decisions on the spatial and temporal design of any proposed marine protected areas. This stresses the point that by using different technologies

as well as analytical methods, many more questions can be addressed and answered, than that based on data and/or species life stages already available. Camphuysen et al. (2012) list an array of devices to improve behavioural studies (e.g. accelerometers, stomach temperature loggers, depth recorder), many of which could greatly improve our understanding of seabird biology. The exact technology used clearly will depend on a species' biology and behaviour as well as study location as to what is possible.

As pointed out earlier, there are still a variety of other environmental parameters to be investigated in relation to seabird distribution, and albatrosses in particular, as I have not been able to address so far. Since most of the parameters subject to investigation are actually proxies for prey distribution or availability (Vilchis et al. 2006; Bost et al. 2009) it would be valuable to more directly investigate how fish (and other prey items) are actually distributed in relation to the birds. However, currently the data needed for such an analysis are scarce, and collecting such data will prove equally if not more challenging than that posed by simply following the birds. Clearly, the technology and its applicability is likely to dictate how much progress is made in this field for the foreseeable future.

Finally, given that it is likely that protected areas will be implemented within at least some areas identified as important for the study species, monitoring will be important to assess whether such conservation measures work (e.g. Pichegru et al. 2012). Additional tracking studies for example could provide information as to whether albatrosses prefer fishery exclusion zones if they follow additional food sources as provided by commercial fisheries, or if they remain within no-take zones because of improved resources. Ultimately, the course of action we take is dependent on how we view the future, either one in which we have emptied the oceans both of their fish and their birds, or one in which it is still possible to marvel at an albatross as it sets off for a flight across the breadth of the Pacific Ocean.

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